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THE EARLY EMBRYOLOGY AND PLACENTATION OF PROCAVIA CAPENSIS

BY

IRENE STURGESS

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EVOLUTION OF THE WING-PATTERN IN PALAEARCTIC SATYRIDAE. IV. POLYMORPHIC RADIATION AND PARALLELISM

BY

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(Entomological Laboratory, State University of Leningrad.)

(With 263 text-figures.)

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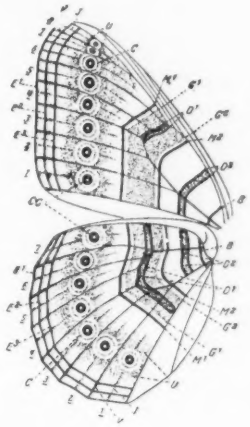
INTRODUCTION.

Three papers were published previously by the present writer (1929, 1931, 1935) containing a morphological analysis of the wing-pattern of nine Palaearctic genera of Satyrid butterflies. The indicated genera form a natural group. Every of them has been shown to derive its wing-pattern from the Nymphaloid prototype constructed by the writer (1924) and about eighty evolutionary series illustrate the derivation. When the whole of the material is reexamined some general principles emerge which seem to be worth of notice. There are mainly two of them termed polymorphic radiation and parallelism in the subsequent description. None of them is new of course. The former is as old as the theory of evolution and does not differ essentially from Darwin's divergency of charactere. The latter though of a more recent appearance in biological literature has been dealt with by a number of workers. But it is of interest first to show that the study of wing-pattern is most closely connected with the general concepts of evolution and thus to illustrate the latter by totally new facts. Secondly an attempt is made by the writer to prove that the two above principles are deeply interdependent and that none of them is likely to lead to any large scale morphological diversity without another's being at work.

CHAPTER I.

REALISATION OF THE NYMPHALOID PROTOTYPE IN THE NINE GENERA OF PALAEARCTIC SATYRIDS.

One of the most salient features of the wing-pattern prototypes is that they are never represented totally in any living form. Their components are distributed among several of them, and to show the realisation of the prototype in a genus one has to select from the latter a number of respective forms and by putting together all their prototypical characters to obtain a hypothetical generic



Figs. 1—2. Prototype of the wing-pattern of Nymphaloid families of Lepidoptera (Nymphalidae, Satyridae, Amathusiidae, Morphidae, Brassolidae).

B — Basalis	G^1 — first Granulata
C — Circulus	G^2 — second Granulata
D^1 — first Discalis	*J* — Intervenosa
D^2 — second Discalis	M^1 — first Media
E^1 — first Externa	M^2 — second Media
E^2 — second Externa	*OC* — eye-spots
E^3 — third Externa	*U* — Umbra
	V — Venosa

Dashes under the numbers of marginal cells mean presence of respective eye-spots. The prototype corresponds to the formula:

$$\frac{E^1\ E^2\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ 7\ 8)\ U\ M^1\ M^2\ G^1\ G^2\ D^1\ D^2\ B\ |\ V\ J}{E^1\ E^2\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ 7\ )\ U\ M^1\ M^2\ G^1\ G^2\ D^1\ D^2\ B\ |\ V\ J}$$

Indexes above and below the line mean fore and hind wings resp. (SCHWANWITSCH 1924).

or generally group pattern that inevitably resembles the prototype much more closely than any existing species or individual. Nine hypothetical generic patterns have been constructed by this method in the palaearctic Satyridae which are represented in figs. 4—12. Their pattern formulae placed underneath show that in every of them more than a half of the 41 components of the prototype (fig. 2) are present. If now we combine together all the prototypical components of the nine generic patterns a super-generic one is obtained (fig. 3) which is more complete than any of the generic ones. It lacks only two components and shows the degree of the realisation of the Nymphaloid prototype in our group of nine genera.

Let us consider now the generic patterns more closely. First of all the tendency of the proximal components, i.e., D^2 and *B*, to disappear is very potent in them, and *Pararge* is the only genus of the nine in which they have been discovered (fig. 7). Because the indicated components, especially D^2, are rather frequent in Satyrids and allied families their almost total absence in our group should be regarded as peculiar specialisation.

On the other hand the behaviour of E^2 is very interesting. It has disappeared from the patterns of *Oeneis, Erebia, Coenonympha* and *Triphysa* (figs. 5, 10, 11, 12), and though present in the remaining ones it is much inclined in them to atrophy. The fact should be emphasized here that the existence of E^2 in some genera and its absence in others is by no means proportionate to the number of species and the variety of pattern in them. *Erebia* is the largest of our genera and is surpassed by none but *Satyrus* in the variety of pattern. Also *Coenonympha* is a large and very variable genus. In neither *Erebia* nor

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Coenonympha, however, E^2 has been discovered, while in the much less variable *Epinephele* and even in the very small *Aphantopus* it is existing. Consequently the tendency of E^2 disappearance is more potent in *Erebia* and *Coenonympha* (the monotonous *Oeneis* and very small *Triphysa* add nothing to the argument) than in any other genus of the group and is very slight in *Aphantopus.*

As to the remaining components the stability of E^3 and M^1 and the frequency of polynome eye-spot series should be also regarded as typical of the group. The eye-spots are so pronounced that even those of the 7th and 8th forewing cells have been met with in *Pararge* and thus a gap in the formula of the whole family of Satyridae (B.N.S. 1924) is filled up (B.N.S. 1935). The difference between the generic patterns in the number and combinations of absent eye-spots are unimportant and seem liable to disappear if more extensive materials are studied. The absence of Granulatae in most of the genera is also unimportant because of a comparative rarity of these components.

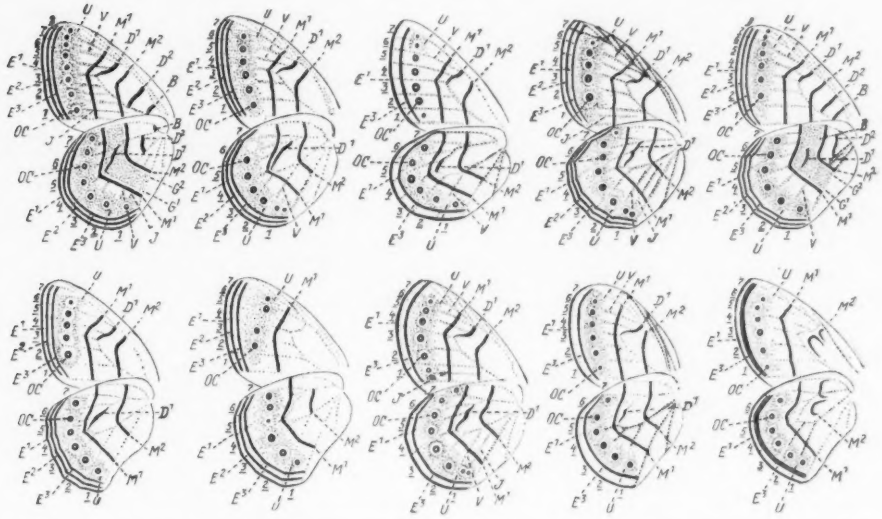
Thus the realisation of the prototype in the individual genera is illustrated by the generic patterns, the latter differ from one another, some of the differences are important, some not so. Thus the generic patterns show on the one hand the tendency of prototypical components to appear in a given genus as revealed at the maximum. On the other hand the differences existing between the generic patterns show, though very incompletely, the distinctive characters of the evolution of individual genera.

The supergeneric pattern of the nine palaearctic genera (fig. 3) derives from the generic ones just as the latter do from the species' and specimens' patterns. Naturally it is more complete than any of the generic ones lacking only three out of the 41 components. Accordingly the supergeneric pattern shows the comparative stability of the prototypical components in the total of the nine genera group, i.e. the components absent from it, namely Granulatae of the forewing, are evidently the least constant in the group in question.

CHAPTER II.

COMPARATIVE ANALYSIS OF THE MODIFICATIONS OF PATTERN COMPONENTS.

To prove the existence of prototypical components in a given genus is mostly but a small fraction of the work on wing-pattern while its main amount is the study of the evolution of individual components. Every of the latter may evoluate in different sometimes in rather many directions. This phenomenon is widely known as divergency of characters. The facts dealt with in the present work do not exactly correspond with the last term, and for the above type of evolution the term of polymorphic radiation or polymorphosis will be used.



Figs. 3—12. Ten hypothetical patterns showing the occurrence of pattern components in respective genera.

3—super-generic pattern consisting of all the components recorded in the nine genera of palaearctic Satyridae

$$\frac{E^1\ E^2\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ 7\ 8)\ U\ M^1\ M^2\ —\ —\ D^1\ D^2\ B\ |\ V\ J}{E^1\ E^2\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ 7\ )\ U\ M^1\ M^2\ G^1\ G^2\ D^1\ D^2\ B\ |\ V\ J}$$

4—Protosatyrus

$$\frac{E^1\ E^2\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ —\ —)\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ V\ —}{E^1\ E^2\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ —\ —\ )\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ V\ —}$$

5—Protoeneis

$$\frac{E^1\ —\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ 7\ —)\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ V\ —}{E^1\ —\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ —\ )\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ V\ —}$$

6—Protomelanargia

$$\frac{E^1\ E^2\ E^3\ OC\ (—\ 2\ 3\ 4\ 5\ 6\ —\ —)\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ V\ J}{E^1\ E^2\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ 7\ )\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ V\ J}$$

7—Protopararge

$$\frac{E^1\ E^2\ E^3\ OC\ (—\ 2\ 3\ 4\ 5\ 6\ 7\ 8)\ U\ M^1\ M^2\ —\ —\ D^1\ D^2\ B\ |\ V\ —}{E^1\ E^2\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ —\ )\ U\ M^1\ M^2\ G^1\ G^2\ D^1\ D^2\ B\ |\ V\ —}$$

8—Protepinephele

$$\frac{E^1\ E^2\ E^3\ OC\ (—\ 2\ 3\ 4\ 5\ 6\ —\ —)\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ —\ —}{E^1\ E^2\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ —\ )\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ —\ —}$$

9—Protaphantopus

$$\frac{E^1\ E^2\ E^3\ OC\ (—\ 2\ 3\ —\ 5\ 6\ —\ —)\ U\ M^1\ —\ —\ —\ —\ —\ —\ |\ —\ —}{E^1\ E^2\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ —\ )\ U\ M^1\ M^2\ —\ —\ —\ —\ —\ —\ |\ —\ —}$$

10—Proterebia

$$\frac{E^1\ —\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ —\ —)\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ V\ J}{E^1\ —\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ 7\ )\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ V\ J}$$

11—Protococnonympha

$$\frac{E^1\ —\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ —\ —)\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ V\ —}{E^1\ —\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ —\ )\ U\ M^1\ M^2\ —\ —\ D^1\ —\ —\ |\ —\ —}$$

12—Prototriphysa

$$\frac{E^1\ —\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ —\ —)\ U\ M^1\ M^2\ —\ —\ —\ —\ —\ |\ —\ —}{E^1\ —\ E^3\ OC\ (1\ 2\ 3\ 4\ 5\ 6\ —\ )\ U\ M^1\ M^2\ —\ —\ —\ —\ —\ |\ —\ —}$$

Lettering as in fig. 2, p. 3.

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Its justification will be given in the last chapter. On the other hand a given evolutionary process may occur either in a single genus or species or in several of them. The latter case is the essence of another widely known phenomenon of parallel evolution or parallelism. It will be also considered in the last chapter while here it should be only remarked that the two indicated principles will guide us when reconsidering and classifying the material described in the preceding parts of the present work.

1. EXTERNAE.

There are three Externae in the prototype (figs. 2, 3, p. 3, 4) named first, second and third Externae (E^1, E^2, E^3). No particular interest is attached to the first Externa of palaearctic Satyrids but those of the second and still more of the third one deserve much attention.

A. Second Externa.

It has been mentioned already (p. 4) that the second Externa (E^2) is very much inclined to disappearance and that some genera lack it totally. There are two ways followed by the process. The most common of them is the atrophy in loco, of which the result is to be seen in fig. 13. Another represents a sort of approximation of E^2 to the first Externa (E^1) and subsequent coalescence of the two stripes into a single component E^1+E^2. A status nearing the completion of the process is seen in fig. 14. The final results of the two cannot be distinguished from one another, but since every of them may be traced in the idividuals of one genus starting with the condition of a fully developed E^2 and this has been established in several genera the discrimination is after all quite possible. Parallel series I (figs. 16—23) and II (figs. 24—26) clearly show the meaning of the above. Series I shows that in all the genera of palaearctic Satyridae with the exception of *Aphantopus* there are species in which E^2 has disappeared most likely by atrophy in loco. In *Satyrus, Melanargia, Pararge* and *Epinephele* the process has been observed in fact (l.c. 1929, 1931, 1935), in the genera which like *Erebia* have no E^2 at all (cf. figs. 3—12) it is impossible to say finally whether E^2 disappeared in loco or fused with E^1. But as far as the former way is more frequent than the latter the decision in its favour is more plausible. As to the E^1+E^2 coalescence shown in the series II its very gradual development has been recorded in *Satyrus* and *Melanargia* (l.c. 1929, 1931) and figs. 24, 25 do not represent final stages of the process which would not look different from those figured in the series I but show a status nearing the completion of the evolution when the faint interspaces between the fusing stripes are yet seen. In *Pararge* the process of coalescence

Figs. 13—15. Three forms of E^2 disappearance. 13—by atrophy (*Erebia*); 14—by fusion with E^1 the process not being completed (*Melanargia*); 15—by umbrification (*Epinephele*). Lettering and species names see pp. 3 and 59 resp.

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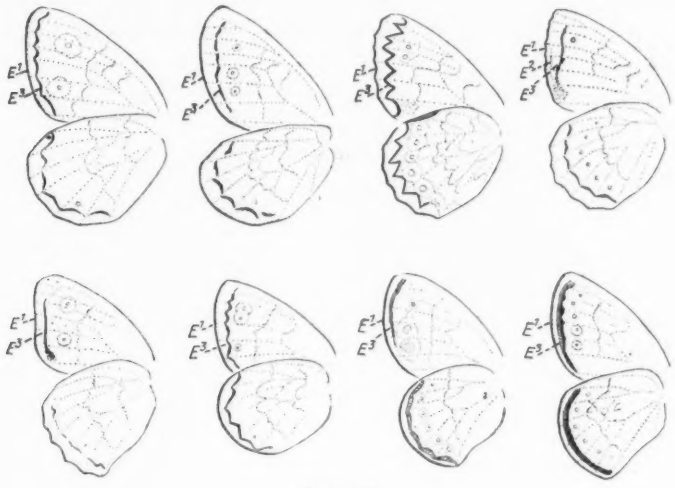
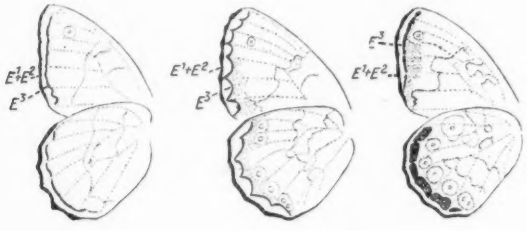


Series I.

Figs. 16—23. Absence of E^2 due to its atrophy in eight genera. Lettering and species names see pp. 3 and 59 resp.



Series II.

Figs. 24—26. Absence of E^2 due to its fusion with E^1 in three genera. Lettering and species names see pp. 3 and 59 resp.

has not been recorded but some other data not to be repeated here (cf. l.c. 1935, p. 151) lead to the conclusion that the terminal stripe seen in fig. 26 represents most likely an E^1+E^2. There is some suspicion that the same fusion takes place also in *Epinephele* but no final proof of this has been obtained.

A third process observed in E^2 may be called umbrification (fig. 15). The stripe becomes broad, suffused along its proximal border, loses its intense pigmentation and begins somewhat to resemble the Umbra of the prototype (*U* in figs. 1, 2). The modification does not result in a total loss of the component, but since the other two Externae remain unaltered the general condition of the terminal zone becomes peculiar. The modification has been recorded in four genera as it is shown by figs. 27—30 of the parallel series III (p. 9).

The modifications of the second Externa not being numerous demonstrate, however, most clearly the work of the two leading principles of the evolution of wing-pattern which are briefly referred to already (p. 3). The second Externa may evoluate in three directions (figs. 13—15). This may be described as p o l y m o r p h i c[1] r a d i a t i o n or polymorphosis, i.e., radiation leading to many forms. The word radiation is preferred to the older divergency on account of the fact that by the latter a repeated branching is meant in every given part of the evolutionary process. This is not the case of the present material where the development of every modification starts from the prototype but no subsequent branching is recorded. On the other hand the fact that the atrophy of E^2 in loco, its fusion with E^1 and its umbrification occur each in several genera (figs. 16—28) is a most typical example of the well known phenomenon of parallel evolution or p a r a l l e l i s m.

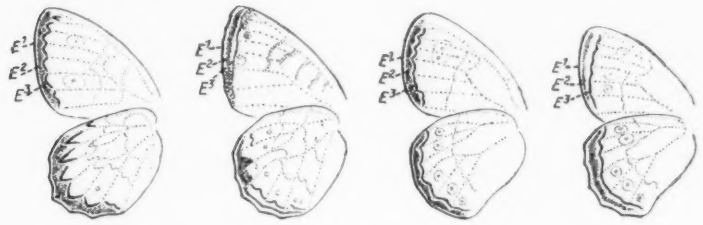
B. T h i r d E x t e r n a.

The third Externa (E^3) is considerably more liable to modifications than the other two, and being besides one of the most constant components it plays accordingly an important rôle in the general composition of a great many patterns.

The most interesting modifications of the third Externa occurring in our genera are those of different ways of curvation which undergo the cell-portions of the stripe.

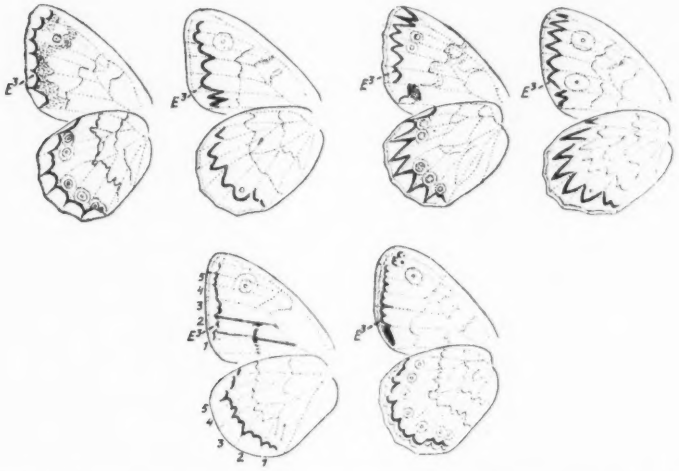
In fig. 31 (*Melanargia larissa*) every of them is regularly curved in thus being of concave shape. In fig. 33 (*Melanargia syllius*) the direction of curvation is the same but the cell-portions are shaped differently, they are sharply bent at the middle and may be therefore described as cuneiform. In the anterior cells of the fore wing and in the middle ones of the hindwing they

[1] The word polymorphic should be preferred to the previously used (B.N.S. 1940) diamorphic.



Series III.

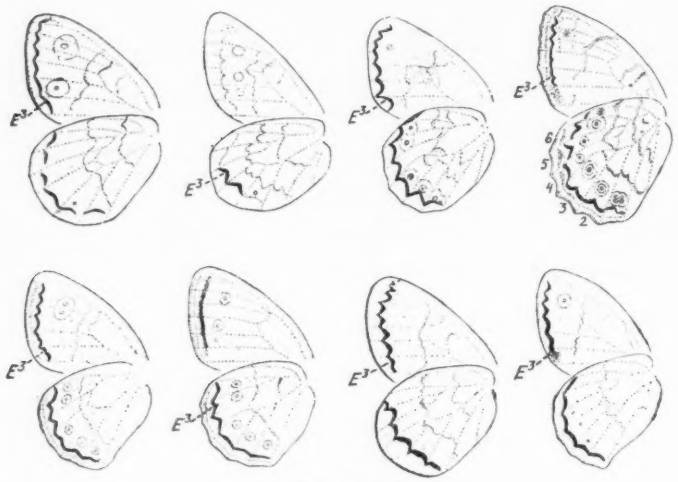
Figs. 27—30. Umbrification of E^2 in four genera. Lettering and species names see pp. 3 and 59 resp.



Figs. 31—36. Six antimere forms of E^3 cell-portions. 31—concave arcuate (*Melanargia*); 32—convex arcuate (*Satyrus*); 33—concave cuneiform (*Melanargia*); 34—convex cuneiform (*Satyrus*); 35—concave bi-arcuate (forewing *Epinephele*, hindwing *Erebia*); 36—convex bi-arcuate (*Pararge*). Lettering and species names see pp. 3 and 59 resp.

are particularly elongated. Fig. 35 represents a combination of two butterflies —the forewing belongs to *Epinephele narica* while the hind one to *Erebia embla*. It has been done so because the modification of E^3 to be seen in them is not frequent and has been nowhere met in such a pronounced condition nor even in the not figured wings of the same specimens. The essence of it is that the stripe forms two bent in curvations in every cell and the modification is termed concave biarcuate. Its best representation is seen in the 1st and 2nd cells of the hindwing and in the 2nd and 3rd ones of the forewing.

Let us now pass on to the three figures placed to the right from the above described ones. It is easy to see in them again the curved (fig. 32), cuneiform (fig. 34) and bi-arcuate (fig. 36) forms of cell-portions. Their most remarkable pecularity, however, is that the direction of their curvation is just as opposite

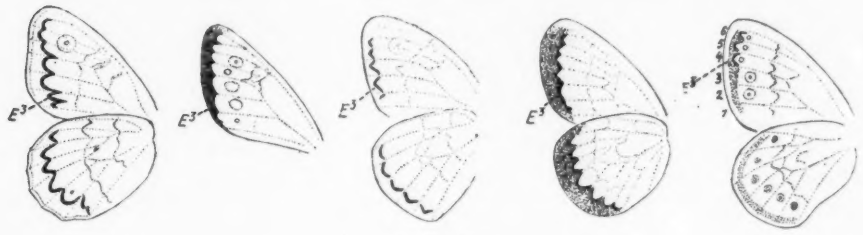


Series IV.

Figs. 37—44. Concave form of the cell-portions of E^3 in eight genera. Lettering and species names see pp. 3 and 59 resp.

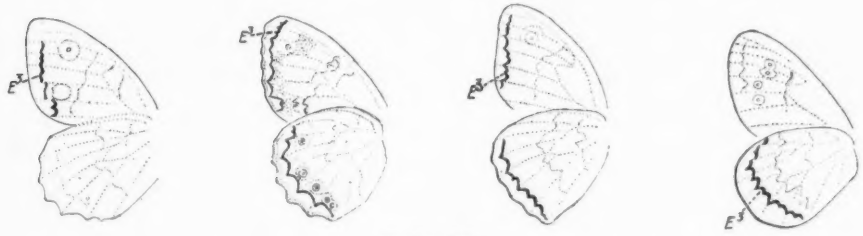
to that of their left neighbours. The cell-portions in figs. 32, 34, 36 should be termed convex arcuate, convex cuneiform and convex biarcuate resp. Thus we see that the third Externa cell-portions evoluate in six different directions, and this is a considerably better example of polymorphic radiation than the modifications of the second Externa. The indicated principle does not cover, however, the whole of the interdependence of the six E^3 forms. The fact is that every concave condition has its exact counterpart in the convex series. Concave arcuate corresponds with the convex arcuate and so on. Resembling the interrelation of the left and right halves of a bilateral body this state of the things differs from it in the face that the corresponding conditions first are both located in a single lateral appendage of the body and second they exist in different specimens. I have termed the se corresponding pairs isomere (1931, p. 331) but now I think that the term antimere should be preferred and the phenomenon itself may be termed a n t i m e r i s m.

Like the modifications of the second Externa those of the third one may occur in several genera each. Series IV (figs. 37—44, p. 10) shows that the concave form of E^3 cell-portions occurs in eight genera out of the nine being unrecorded only in *Triphysa*. In some of them as e.g. in *Satyrus, Melanargia, Erebia* and *Coenonympha* all or most of the cell-portions are more or less arcuate too, in others the arcuate shape is seen but in a few cells (*Pararge, Epinephele, Aphantopus*) or is not seen at all (*Oeneis*), but this is of secondary importance, and it is out of doubt that the concave form of the E^3 cell-portions is one of the most frequent modifications occurring in our group.



Series V.

Figs. 45—49. Convex form of E^3 cell-portions in five genera. Lettering and species see pp. 3 and 59 resp.



Series VI.

Figs. 50—53. Concave bi-arcuate form of E^3 cell-portions in four genera. Two wings in fig. 52 belong to different specimens. Lettering and species names see pp. 3 and 59 resp.

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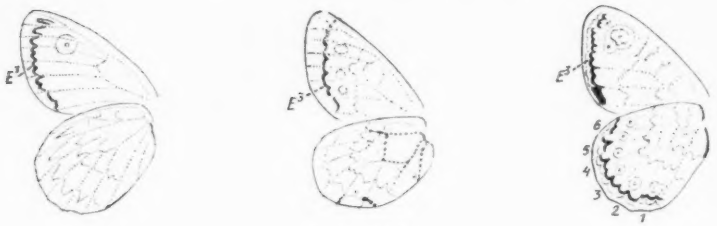
Somewhat different is the case of its antimere, i.e., convex E^3 cell-portions. As the series V (p. 11) shows it occurs only in five genera and has not been recorded in the four others. Out of the former in *Oeneis* and *Erebia* (figs. 46, 48) the stripe has lost its strial character and represents but a boundary of a dark trans-E^3 zone, while in *Triphysa* (fig. 49) it has undergone a peculiar duplication owing to the appearance of silver glittering scales in the middle of it (l.c. 1935, p. 241) and only the proximal half shows the convex shape of its cell-portions in the three anterior cells, and in these latter the process seems to depend upon the approximation of the eye-spots to the stripe. Nevertheless in all the figures 45—49 it is typical enough, and it should be added still that convex modification being in general less frequent than the concave one is particularly typical of the genus *Satyrus* in which convex cell-portions are much more common than concave ones.

Bi-arcuate forms of E^3 cell-portions occur much more seldom than uni-arcuate ones. The concave bi-arcuate condition has been discovered in four genera (series VI, p. 11) while its convex antimere only in three (series VII). These numbers are not very small in themselves but the fact is that in some genera I have succeeded to discover the modifications in question but in a very few cells of a single wing (figs. 50, 51, 55). *Pararge* is the only genus exhibiting a bi-arcuate modification in most of the cells of both wings (fig. 56) but the very shape of its cell-portions is not very typical, some of them



Series VII.

Figs. 54—56. Convex bi-arcuate form of E^3 cell-portions in three genera. Lettering and species names see pp. 3 and 59 resp.

differing but slightly from the uni-arcuate concave modification as e.g. that in the 5th hindwing cell. The same is the case of *Oeneis* concave bi-arcuate ones (fig. 55). Thus the third Externa shows six main directions of polymorphic radiation which are combined into three pairs by the peculiar phenomenon of antimerism. Four of them show questionless intergeneric distribution and thus form one of the best examples of parallelism.

2. EYE-SPOTS.

The essential feature of the ocellar or eye-spot series is that belonging to the transverse system of pattern components it differs from the rest of the latter in the fact that if the individual eye-spots are homologically comparable to the cell-portions of common stripes they show much more independence from one another than cell-portions of any stripe. Most of the modifications of eye-spots are those of their combinations, size and position.

A. Combinations.

Though in general the palaearctic Satyrids may be described as multiocellate forms the polynome ocellar series occurs less often than oligonome ones. The most polynome series has been recorded in *Erebia afra* (fig. 57) that lacks only the eye-spots of the 7th and 8th forewing cells. The transition to oligonome status may follow several ways. The most interesting of them is that starting with the forewing where as in *Melanargia parce* (fig. 58) the 4th and 5th eye-spots prove to be more constant than the rest. A further elimination to be seen in *Melanargia larissa* (fig. 59) shows that the 4th forewing eye-spot is less constant than the 5th. The hindwings of the indicated species still exhibit rather polynome series though the 7th hindwing spot is already absent in fig. 58 and is followed by the 4th one in fig. 59 the latter being diminished still in fig. 58. Figs. 66—70 forming our parallel series VIII (p. 14) show that the above condition of multiocellate hindwing and pauciocellate forewing

THE WING-PATTERN IN PALAEARCTIC SATYRIDAE

Figs. 57—65. Different ways of combinative disappearance of eye-spots corresponding to the formulae:

57. 1 2 3 4 5 6 — — (*Erebia*),
1 2 3 4 5 6 7

58. — — — 4 5 — — — (*Melanargia*),
1 2 3 4 5 6 —

59. — — — — 5 — — — (*Melanargia*),
1 2 3 — 5 6 —

60. — 2 — — 5 — — — (*Satyrus*),
— 2 — — 5 — —

61. — 2 — — 5 — — — (*Satyrus*),
— 2 — — — — —

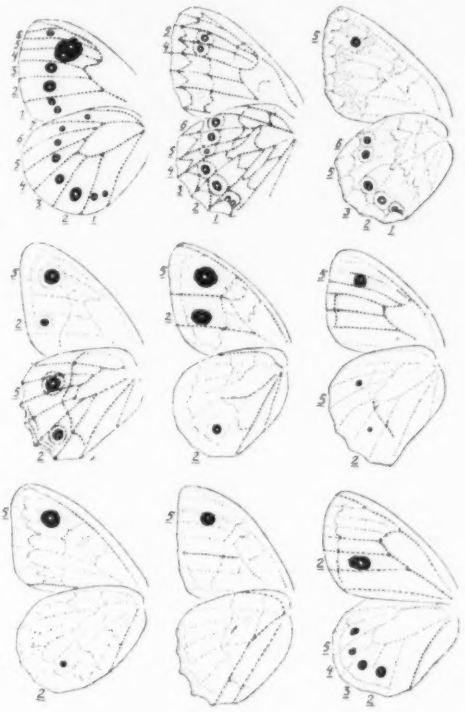
62. — — — — 5 — — — (*Epinephele*),
— 2 — — 5 — —

63. — — — — 5 — — — (*Satyrus*),
— 2 — — — — —

64. — — — — 5 — — — (*Satyrus*),
— — — — — — —

65. — 2 — — — — — — (*Oeneis*).
— 2 3 4 5 — —

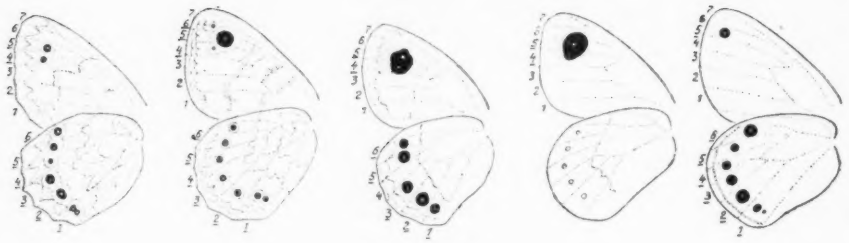
Lettering and species names see pp. 3 and 59 resp.



is typical and its bearers have been discovered in five genera. It should be remarked that in *Erebia hades* (fig. 69) the hindwing does not show fully developed eye-spots but only ocellar markings—patches of white on the dark background. Though the relation of the indicated markings to fully formed eye-spots is not fully analysed yet their homologous interdependence is doubtless as I have shown it elsewhere (1932, p. 437), and therefore *Erebia hades* may be included into the series VIII. On the other hand it should be emphasised that the predominant character of the 5th eye-spot in the forewing is readily seen in *Pararge, Erebia* and *Coenonympha* while *Melanargia* and *Aphantopus* show the already noticed decrease and final disappearance resp. of the 4th hindwing spot.

It should be remarked here that in spite of the fact that the above eliminations of eye-spots undoubtedly belong to combinative evolution only a very few of many imaginable combinations do exist in fact.

A further elimination leads to typical oligonome series in which the 2nd and 5th eye-spots of both wings represent the only components. Fig. 60 shows a "symmetrical" combination exemplified by *Satyrus parisatis* in which the indicated eye-spots are more or less equally pronounced on both wings. In *Satyrus autonoe* (fig. 61) two eye-spots are preserved in the forewing only



Series VIII.

Figs. 66—70. Predominance of the 4th and 5th eye-spots on the forewing and nearly complete ocellar series on hindwing in five genera. Lettering and species names see pp. 3 and 59 resp.

while from the hind one the 5th has disappeared. Very interesting is *Epinephele janira* (fig. 62) in which just a reverse combination may be seen, i.e. the 2nd eye-spot has disappeared from the forewing but is retained in the hind one. *Satyrus arethusa* (fig. 63) is still more oligonome and its series consists of two components only, 5th in the forewing and in the hind one. Finally *Satyrus pisidice* (fig. 64) may be described as uniocellar form having only the 5th forewing spot, which is however very well pronounced. The forms of this type or at least approximating to it are very frequent in palaearctic Satyrids and some of them may be seen in the parellel series IX (p. 17). The same is seen in many other patterns (figs. 234, 235, 244, 245, 248, p. 43). On the other hand the preponderance of the 2nd eye-spot in the oligonome forewing series belongs to the commonest characters of our group and its examples are also numerous. As it has been noticed the 5th eye-spot is often accompagnied by the 4th one but the latter never appears without the former. As to the other eye-spots their preponderance occurs but seldom and the respective forms like *Oeneis walkyria* (fig. 65) look somewhat strange as compared to the very perfect proportions of patterns represented in figs. 60—64. It is interesting to summarize the above ocellar combinations by means of the formulae:

1) *S. parisatis* (f. 60)

—	2	—	—	5
—	2	—	—	5

2) *S. autonoe* (f. 61)

—	2	—	—	5
—	2	—	—	—

3) *Ep. janira* (f. 62)

—	2	—	—	—
—	2	—	—	5

4) *S. arctusa* (f. 63)

—	—	—	—	5		
—	2	—	—	—	—	—

5) *S. pisidice* (f. 64)

—	—	—	—	5
—	—	—	—	—

The combinative character of the differences between the five above ocellar series is obvious.

Now from a purely structural point of view all the eye-spots of the prototype (p. 3) are quite alike except a few anterior ones which are small owing to the narrowness of their cells. Be the combinations of eye-spots free there would be much more of them in oligonome series than the above five. But this is not the case and the emphasis should be laid upon the fact that the really existing oligonome ocellar combinations represent but a small fraction of a great number of them that might be theoretically calculated. The 2nd and 5th eye-spots of both wings show a much greater constancy in the evolution than all the remaining ones, and hence the principle of combination, so clearly demonstrated by the above formulae, is restricted to some very narrow channels. The indicated restrictions are however supported by the venation criterion. The numerical system of cell designations is adopted in this work only because of its simplicity the latter being necessary when the pattern system complex in itself and dependent upon venation is dealt with. But according to the generally accepted Comstock's terminology the cells numbered 2 and 5 are undoubtedly homologous in both wings as they lie behind the 1st cubital and 1st median veins resp. It is likely that there are some developmental differences between the 2nd and 5th cells of both wings on the one hand and all the remaining ones on the other. It should be also remarked that the presence of the 2nd and 5th eye-spots affords an especial beauty to the wing that is hardly attainable in other ocellar combinations.

Finally it is worth of notice that the stability of the above two eye-spots occurs in other groups too as e.g. in the Nymphalid genus *Junonia* while the 5th eye-spot is replaced by the 6th one in the hindwings of *Prepona* and *Catagramma* and by the 7th one in those of the Brassolid family.

B. Expansion.

The size of individual eye-spots may increase greatly, and there are several ways of the process. In *Satyrus abramovi* (fig. 71) the 2nd and 5th eye-spots have so expanded that every of them enters far into the neighbouring cells. Nearly the whole diameter of the 4th cell is covered by the 5th eye-spot. A typical feature of *abramovi* eye-spots is the absence of supplementary pupils in them. The latter are, however, present in the 3rd and 4th cells of *Satyrus dryas* (fig. 72). Eye-spot is a too complicated component to say at present why supplementary pupils are acquired in one case and do not appear in another, but the fact is that in *abramovi* and *dryas* two different forms of ocellar expansion are exemplified. A third one consisting of a marked elongation restricted exactly to a single cell occurs in *Epinephele wagneri* (fig. 73). This modification exists on the upperside only while the underside shows rather a

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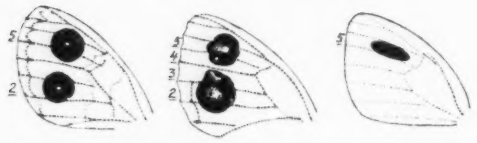


Figs. 71—73. Three forms of eye-spots expansion. 71—no formation of supplementary pupils (*Satyrus*); 72—supplementary pupils in the 3rd and 4th cells (*Satyrus*); 73—elongation within a single cell (*Epinephele*). Lettering and species names see pp. 3 and 50 resp.

prototypical status in the same component (B.N.S. 1935, p. 177). The three described forms of expansion may be also regarded as an example of polymorphic radiation. In the above described form they are not frequent and there are no corresponding parallel series at my disposal, but moderate degrees of the 5th eye-spot increase are seen in some forewings (figs. 235, 245).

C. Subdivision.

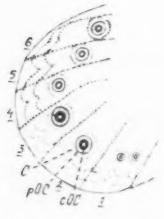
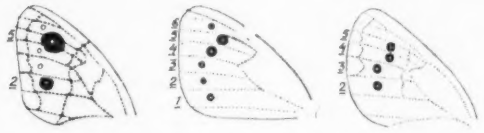


Fig. 74. Formation of false Circuli (*pOC*) in *Pararge megaera* L. due to depigmentation of sub-peripheric zones of eye-spots. *C*—Circulus, *cOC*, *pOC*—central and peripheric zones of eye-spots which are left dark.

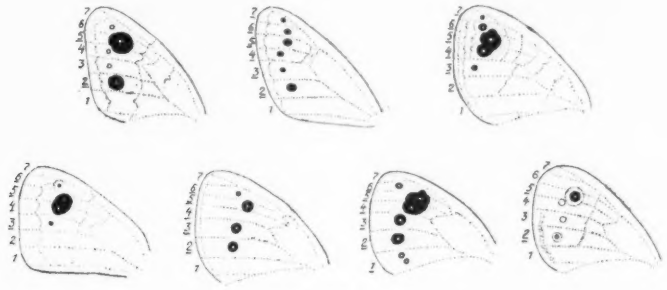
A peculiar modification has been described by me in *Pararge* (1935). It consists of a depigmentation of submarginal zone resulting in a separation of a peripheric ring (*pOC* in fig. 74) from the central area (*cOC*) of the eye-spot. Because the genuine Circuli (*C*) are also present, the ocellar pattern grows very complicated. The modification is however, far from being common and has been met with in none of our nine genera but *Pararge* though it does occur in some other groups (l.c. p. 154).

D. Erebisation and anti-erebisation.

By erebisation the basipetal shifting of the 5th and sometimes also of the 4th eye-spots is meant. Three forms of it may be discerned. First the 5th eye-spot may dislocate alone its neighbours being stationary. This is to be seen in fig. 75. The fact of the presence of white ocellar markings instead of eye-spots in the 4 the and 6th cells does not impair the evidence of the process. Second the 5th eye-spot may be followed by the 4th one which, however, advances less than the former (fig. 76). It should be noticed that the 6th eye-spot in fig. 76 may be regarded as stationary and thus evidently the 5th eye-spot affects much more its posterior neighbour than the anterior one. And finally the 4th and 5th eye-spots may be dislocated both together none of them advancing more than another (fig. 77). Owing to the absence of the 6th eye-



Figs. 75—77. Three forms of erebisation. 75—5th eye-spot shifted basipetally, neighbouring ocellar markings stationary (*Satyrus*); 76—5th eye-spot followed by the 4th one (*Erebia*); 77—4th and 5th eye-spots equally dislocated basipetally (*Erebia*). Lettering and species names see pp. 3 and 59 resp.

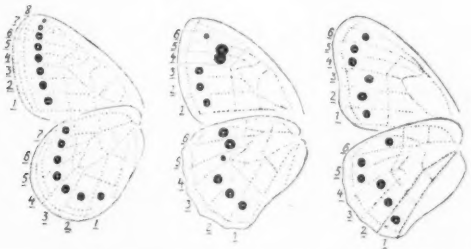


Series IX.

Figs. 78—84. Erebisation (basipetal dislocation of the 5th eye-spot) on the forewing in seven genera.

Series X.

Figs. 85—87. The same on the hindwing in three genera. Lettering and species names see pp. 3 and 60 resp.



Figs. 88—90. Diagrams of erebisation and anti-erebisation. 88—prototypical position of eye-spots; 89—erebisation on both wings: 4th and 5th eye-spots shifted basipetally (forewing after *Erebia* hindwing after *Aphantopus*); 90—anti-erebisation: 4th and 5th eye-spots shifted basifugally, 3rd and on the hindwing 6th ones basipetally (forewing after *Triphysa*, hindwing after *Coenonympha*).

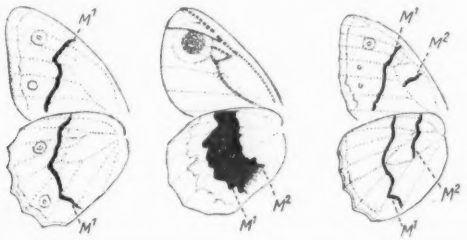
spot this example is less typical than one might desire but the essence of the thing cannot be doubted.

The forewing erebisation, to say nothing of its above three forms, belongs to the commonest modifications in our group, and it is rather difficult to find an undoubtedly non erebised ocellar series. Accordingly the parallel series IX is very complete. The genera of *Melanargia* and *Triphysa* are the only two in which this process has not been recorded.

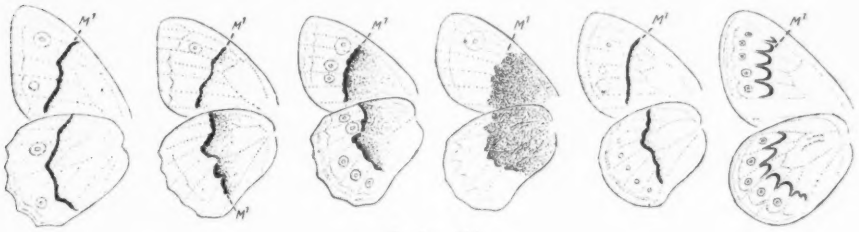
On the hindwing some dislocations in the eye-spot series are met with which may be also regarded as erebisation. So, e.g. the hindwing represented in fig. 89 shows a condition occurring in *Aphantopus*. It is evident that the 5th eye-spot is markedly shifted in the basipetal direction being followed in a way by the 4th one while that of the 6th cell is but slightly displaced from its normal position, if at all. Thus the curvation of the anterior part of the ocellar series on the hindwing does not essentially differ from that on the forewing if being compared to fig. 76. The hindwing erebisation does not seem to be frequent and has not been discovered in any other form of our Satyrid genera.

It is very interesting that in *Coenonympha* and *Triphysa* dislocations have been discovered in the ocellar series which are inverse to erebisation and may be hence termed anti-erebisation. Fig. 90 represents *Triphysa* condition in the forewing and that of *Coenonympha* in the hind one. Let us begin with the latter. Its 4th and 5th eye-spots have much approached to the wing-margin, while those in the 6th, 3rd and somewhat less so in the 2nd ones are shifted in the opposite direction. The distance thus resulted in between the 5th and 6th spots is very wide. On the forewing, i.e., in *Triphysa* the condition though less pronounced is essentially the same: the 4th and 5th eye-spots are somewhat dislocated basifugally, while the 3rd one has shifted basipetally. The distance between the 3rd and 4th eye-spots has become very considerable. It should be remarked here that fig. 90 represents a purely artificial combination as neither *Coenonympha* shows the described process in its forewing nor *Triphysa* in the hind one.

Now an interesting comparison may be made of the two processes dealt with. Fig. 88 represents ocellar series in its prototypical condition. In fig. 89 erebisation in both wings and in fig. 90 anti-erebisation in the same are to be seen. It is evident that they may be regarded as antimere processes like acquisition of concave and convex shapes in the E^3 cell-portions. On the other hand the processes in question may be both described as a tendency of the 4th and 5th eye-spots to be located differently than their posterior and anterior neighbours. According to Comstock's venational terminology the 4th and 5th cells of our practical system of numeration are just lying between the three branches of the Median vein. Consequently homologically different venational areas of the wing also differ in their pattern components, and thus the present case reveals again the interdependence of venation and pattern system.



Figs. 91—93. Three ways of combinative disappearance of Mediae. 91—M^1 present M^2 absent on both wings (*Satyrus*); 92—M^1 and M^2 present on hindwing absent on forewing (*Erebia*); 93—M^1 as in 91, M^2 vanished from postdiscal cells in both wings (*Satyrus*). Lettering and species names see pp. 3 and 60 resp.



Series XI.

Figs. 94—99. Presence of M^1 absence of M^2 on both wings in six genera.

3. MEDIAE.

The diversity of modifications described in the foregoing sections is far inferior to that of the Medial system of stripes the latter undoubtedly being the most variable components of the prototype.

A. Combinations.

The two components which the Medial system is built of, i.e., the first (M^1) and second (M^2) Mediae exhibit different degrees of constancy and even the fore and hindwing parts of a given stripe may differ from one another with regard to this.

It is evident that the first Media is much less inclined to vanish than the second one. A vary common condition is exemplified by fig. 91 where M^1 is pronounced and M^2 totally absent. Parallel series XI shows the occurence of M^1 in six genera to which two more may be added (*Oeneis* and *Pararge*) if taking into account the upperside too (cf. figs. 240, 241 in the series XXVI).

Another combination less frequent than the preceding one is the preservation of both Mediae on the hindwing coupled with their disappearance from the fore one (fig. 92). As series XII shows its exact representation has been discovered only in *Satyrus* and *Oeneis* where no trace of M^1 and M^2 is seen

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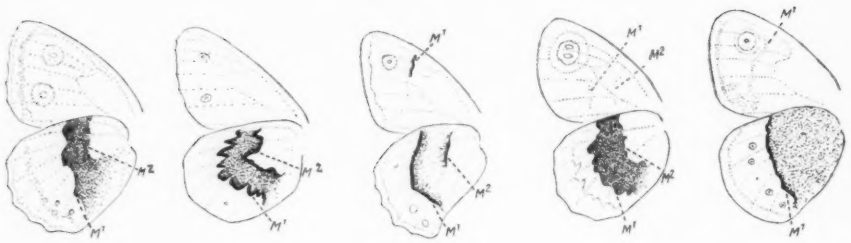


Series XII.

Figs. 100—104. Presence of M^1 and mostly of M^2 on hindwing, and absence of degenerescence of M^1 and M^2 on forewing in five genera. Lettering and species names see pp. 3 and 60 resp.

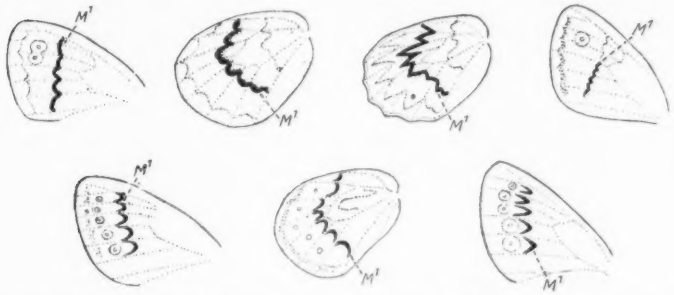
on forewings. Three remaining genera require some explanation. In *Epinephele davendra* (fig. 102) the forewing M^1 is still existing in the anterior cells while its rest is yellow—a sign of approaching disappearance. In *Erebia cyclopius* (fig. 103) the forewing (which is darkened in the specimen) still shows some faint traces of both stripes. In *Coenonympha arcanioides* (fig. 104) the hindwing is not quite typical owing to the absence of M^2, on the forewing a faint yellow trace of M^1 is still seen, M^2 being totally absent. The two first named specimens undoubtedly represent the beginning of the process completed in *Satyrus* and *Oeneis* and hence may be placed in our parallel series. The *Coenonympha* case is somewhat at variance from the rest owing to the disappearance of M^2 from the hindwing. Because, however, its M^1 shows an evident degenerescenceon the forewing and none on the hind one the genus may be tentatively included into the parallel series. It is thus evident that the tendency towards to $\frac{- \; -}{M^1 \; M^2}$ formula is less pronounced than that towards $\frac{M^1 \; -}{M^1 \; -}$. Still less frequent is the disappearance of the postdiscal portions of M^2 (fig. 93). It has been recorded only in *Satyrus* but because of its similarity in both wings the combination thus resulted in deserves attention.

4. FIRST MEDIA.

Let us now pass on to the first Media and to examine first the modifications of its cell-portions and then the evolution of the whole of the stripe.

A. Cell-portions.

The cell-portions of the first Media may be convex arcuate as it is the case in some species of *Erebia* (figs. 105, 106) while the antimere concave form of the arcuate modification is very well exemplified by *Triphysa* (figs. 109,



Figs. 105—111. Five forms of M^1 cell-portions, four of them being antimere (all except 108). 105—106—convex arcuate (*Erebia*); 107—convex cuneiform (*Satyrus*); 108—convex bi-arcuate (*Coenonympha*); 109—110—concave arcuate (*Triphysa*); 111—concave cuneiform (*Triphysa*). Lettering and species names see pp. 3 and 60 resp.

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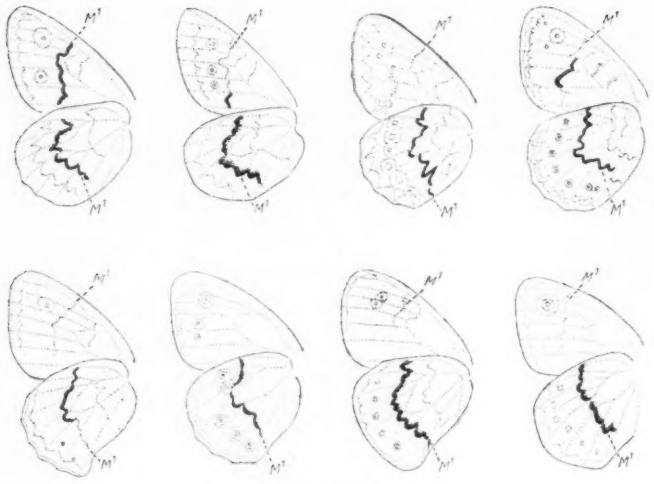
110). Cuneiform convex cell-portions of M^1 have been discovered in a *Satyrus* hindwing (fig. 107) and cuneiform concave in the anterior cells of a *Triphysa* forewing (fig. 111). Finally convex bi-arcuate M^1 cell-portions are to be seen in two forewing cells of a *Coenonympha* (fig. 108) and no concave biarcuate modification has been met with in the Mediae of our group of genera. The most common of the above modifications is undoubtedly convex arcuate. Series XIII shows its occurrence in eight genera, *Triphysa* being the only exception. In spite of the fact that in most of them the modification is restricted to the hindwing and in some genera it occurs only in a few cells (fig. 116), the representation of the phenomenon is quite good. Concave arcuate form is less frequent and series XIV lacks three genera on the one hand while *Oeneis* and *Melanargia* show but indifferent development of the modification on the other. The latter circumstance seems to be counterbalanced by its very complete representation in the three right members of the series. But this should not be overestimated as the great majority of the *Erebia* and *Coenonympha* species belong to the convex M^1 type, while *Triphysa* is a very small genus.

The cuneiform and bi-arcuate types are still less frequent.

It is now interesting to turn back to figs. 105—111 and to compare them with figs. 31—36 (p. 9). Parallelism of the cell-portion forms in E^3 and M^1 is very striking. In both components we have convex arcuate cell-portions (cf. figs. 105, 106 with fig. 32) and concave arcuate ones (cf. figs. 109, 110 with 31). Though the occurrence of the two types is reverse in different components, viz., concave are predominant in E^3 (cf. series IV) and convex in M^1, the fact remains evident that the two stripes are liable to identical "cellular" modifications. Cuneiform convex is seen equally in figs. 107 and 34 (made from the same species of *Satyrus*), cuneiform concave in III and 33 and bi-arcuate convex in 108 and 36. The only of the six types of the cell-portions existing in E^3 and not discovered in M^1 is bi-arcuate concave (fig. 35). Its occurrence in E^3 itself is, however, rather unfrequent (cf. series VI).



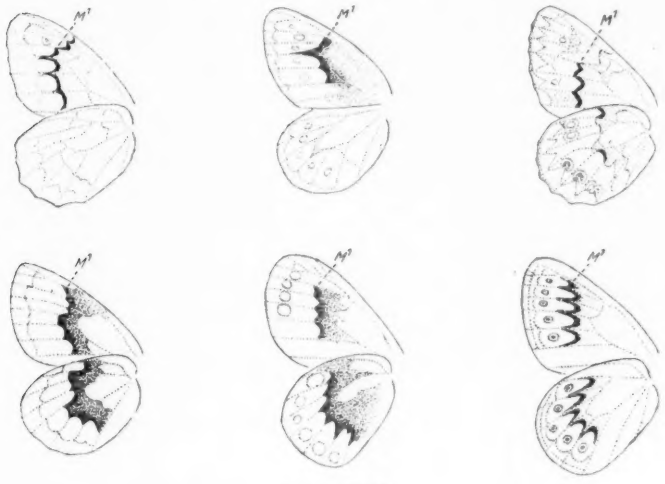
Series XIII.

Figs. 112—119. Convex cell-portions of M^1 in eight genera.

Thus the interdependence of several antimere modifications of E^3 cell-portions is almost totally reproduced in M^1. If the cellular curvations of E^3 do not differ essentially from those of M^1, we have to conclude that parallel modifications may occur not only in different genera but also in different components of a single individual. Fig. 225 (p. 39) with its convex cuneiform E^3 and M^1 cell-portions exemplifies this very well. One more circumstance deserves a notice, however. We have seen that the two main E^3 curvations should be ascribed to differently located basipetal movements. Meanwhile the forms of M^1 represented in figs. 105—111 give the impression of basifugal dislocation restricted either to nervures (fig. 109) or to internervural lines of the cells (fig. 107). From this point of view convex E^3 and concave M^1 correspond to each other because the dislocation develops along the veins in both of them, and as we will see yet a veinous fusion of the two stripes in question is often due to this interdependence. Meanwhile, e.g., convex E^3 and convex M^1 though formally identical (fig. 225) differ from one another in the fact that dislocations are veinous in the former component and interveinous in the latter.

B. General form and position.

The general shape and position of the first Media on the forewing should be described separately from those in the hindwing as the modifications observed in different wings have often nothing in common.



Series XIV.

Figs. 120—125. Concave cell-portions of M^1 in six genera. Lettering and species names see pp. 3 and 60 resp.

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a. *Forewing.*

The evolution of the forewing first Media is represented in figs. 126—146. Fig. 126 placed in the centre shows the prototypical form and position of the stripe while on the periphery some ten final conditions of the evolution are seen each connected with the prototypical centre by a transitionary form. The latter belong either to the same species as the final forms or nearly related ones. The directions of the processes are shown with arrows, the stripe in question is drawn black while the remaining components are made dotted.

Fig. 128 (*Epinephele janiroides*) shows oblique position of the first Media due to the basifugal dislocation of the hind end of the stripe while the anterior one remains more or less stationary. Fig. 127 (*Epinephele wagneri*) represents a good transition from the prototypical status of fig. 126.

In fig. 130 (*Pararge episcopalis*) another form of the oblique position is shown which differs from the preceding one in two respects. First the hind end of M^1 has almost reached the tornus and is irregularly convex in the whole. Second the area proximal to M^1 has grown dark and the component itself has lost its strial character now representing but a limit of a dark area. This form of the first Media is very frequent among exotic genera of Nymphalids and Satyrids, and occurs but seldom in temperate regions. It seems reasonable to consider it as a modification different from the preceding simple acquisition of oblique direction when nothing happens but a slight dislocation. A transitionary condition leading from the prototype towards the *episcopalis* is represented by the related *Pararge pracusta* (fig. 129)

In both preceding cases dislocation is restricted to the hind end of the stripe. The next case is of just as opposite character first because the whole of the stripe is moving, second because the fore end is shifted more than the hind one. The result shown in fig. 131 (*Coenonympha oedippus*) is that the stripe has become rectilinear or even slightly bent in and parallel to the ocellar series. The salient feature of the final condition (fig. 132) is that the anterior end of the stripe has disappeared owing to its contact and subsequent fusion with the circular components. Gradual development of the fusion is described elsewhere (B.N.S. 1935, p. 228—229), but here it must be emphasized that the disappearance of the fore end is due to the fact that it dislocates further than the rest of the stripe. This modification occurs in the hindwing too and will be dealt with in the next section.

The modification shown in fig. 134 (*Satyrus saraswati*) is again reverse to the preceding one as its essence consists of a basipetal shifting of the whole of the stripe without any marked reshaping with the result that in the 3rd cell the component is pressed as it were against the nervure and therefore markedly narrowed. A closely related species of *brahminus* (fig. 133) well connects *saraswati* with the prototype. The modification also belongs to a few affecting both wings and is termed charaxisation owing to its occurrence in a much more pronounced form in the Nymphalid genus *Charaxes*.

The essence of the next four modifications consists of strong alterations of the shape of the first Media which are due to dislocations of definite parts of it.

Fig. 136 (*Pararge achine*) shows a tongue-like outgrowth that depends mainly on a basifugal dislocation of the 4th cell-portion of M^1 followed by those of the 3rd and 5th cells, while the remaining ones are more or less stationary. In fig. 135 (also an *achine*) the tongue is less pronounced.

In fig. 138 (*Melanargia parce*) a very peculiar modification of the first Media is seen termed melanargoid (B.N.S.1931, p. 336) owing to its being typical of the genus *Melanargia*. It consists of a strong basifugal dislocation in the 3rd cell while in the hind part of the 4th one the stripe has shifted a little basipetally. The two portions dislocating in opposite directions are linked by means of a tapering part which lies in the 4th cell and adheres the 4th vein very closely. The almost rectangular projection in the middle and a semicircular form of the anterior part of the stripe are both typical of the melanargoid M^1. A *Melanargia japygia* (fig. 137) fills up the gap between *parce* and the prototype.

Another type of M^1 due to local displacements is shown in fig. 140 (*Pararge egeria*). The stripe forms a very long and sharp denticle along the 4th vein thus the shape of the 4th cell-portion resembling in a way the above modification in *Melanargia*. But the 3rd cell-portion represents something just as opposite to the condition of fig. 138 as instead of being dislocated basifugally it has shifted in the basipetal direction, and therefore broken off from the

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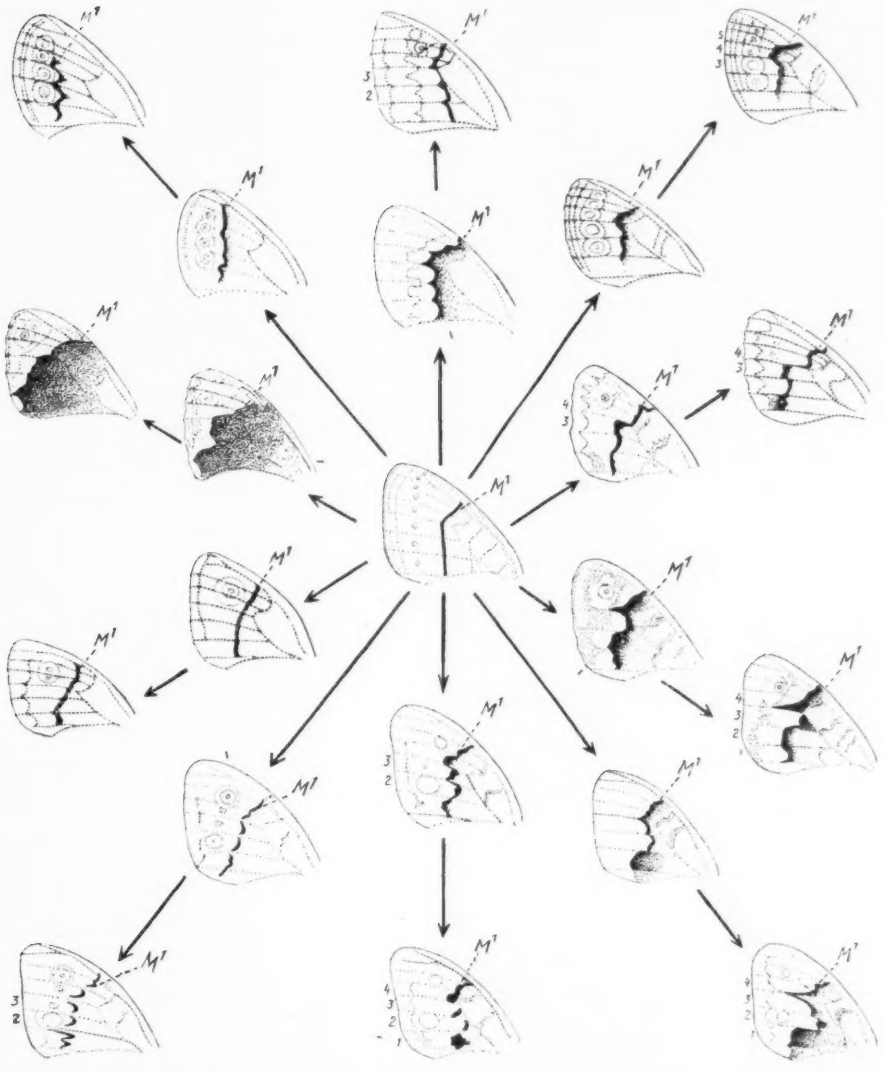

Figs. 126—146. Ten weys of polymorphic radiation in the forewing first Media (M^1) the directions being marked with arrows. 126—prototypical condition; 127—128— oblique position (*Epinephele*); 129—130—still more oblique position (*Pararge*); 131—132—approximation to ocellar series (*Coenonympha*); 133—134—charaxisation (peculiar basipetal shifting) in *Satyrus*; 135—136—tongue-like basifugal protrusion (*Pararge*); 137—138—ladder-like (melanargoid) dislocation (*Melanargia*); 139—140—denticle-shaped dislocation and rupture (*Pararge*); 141—142—another form of the same (*Satyrus*); 143—144—division into several independent parts (*Satyrus*); 145—146—another form of division named "perforation" (*Satyrus*). For species names see p. 60.

4th cell-denticle. The stripe is thus divided into two halves which seems never to be the case of *Melanargia*. The 2nd cell-portion has somewhat shifted basifugally, while the 1st one is seemingly stationary. In another *egeria* (fig. 139) all the described modifications are much less pronounced and there is no division of the component.

M^1 in fig. 142 (*Satyrus anthe*) is similar to that in fig. 140 as the prominent denticle on the 4th vein is typical of both of them. But the resemblance is accompagnied by a number of differences. First of all the denticle is composed of the 4th cell-portion in fig. 140 and of the 4th and 3rd ones in 142 with the result that no rupture of the stripe so typical for the former takes place in the latter. Then the positions of the 2nd and 1st cell-portions are nearly reverse in the two forms. In fig. 140 the stripe is bulged out in the 2nd cell and bent in in the 1st one the two indicated cell-portions lying near by the same level. On the contrary in fig. 142 the 2nd cell-portion is the most proximal while the 1st one occupies a very distal position. Thus it is evident that in spite of general similarity of figs. 140 and 142 essential differences between them are more numerous than resemblances. As to the derivation of the final *anthe* from the prototype another specimen of the same species (fig. 141) serves a good transition between the two.

Now two modifications remain the principal characteristics of which is the division of M^1 into cell-portions. In fig. 144 (*Satyrus bischoffi*) the 3rd and 2nd cell-portions are isolated from their neighbours and thus the stripe though ladder-shaped but still continuous in fig. 143 has dissolved into four pieces in 144.

Quite another type of division occurs in *Satyrus fatua*. In one specimen (fig. 145) the stripe is slightly interrupted on almost every vein crossed by it and the cell-portions are markedly concave. In the final individual (fig. 146) the concavities are much more pronounced and supposing constant the length of every portion the result is that the interspaces dividing them have widened considerably and the stripe now consists of five independent pieces. The result is generally similar to the preceding modification but the differences between the two are to obvious to be discussed.

The described ten modifications of M^1 may be classified under three groups: 1) general dislocations without any strong alteration of form (figs. 128, 130, 132, 134), 2) strong alterations of form due to local dislocations (figs. 136, 138, 140, 142) and 3) divisions (figs. 144, 146).

It is remarkable how very few are examples of parallel evolution found among them. It is true that as series XV shows the oblique position of M^1 occurs in six genera out of nine and the uniformity of the modification in all of them makes the series one of the best examples of parallelism at the disposal. But parallelism of the remaining modifications is of a very narrow scale. Only melanargoid Media may be named here that occurs besides *Melanargia* also in

some *Pararge* forms (series XVI). Meanwhile even charaxisation (fig. 134) cannot be taken into account as *Charaxes* belongs to another family. Thus as matter of fact parallelism in the forewing first Media is restricted to a pair of modifications every of the other forms of the stripe being met with but once. As compared to the wide occurrence of parallelism in the single cell-portions of the same stripe this circumstance deserves notice.

b. *Hindwing.*

There are eight modifications to be considered in this section. The first of them represents a singular curvation of M^1 occurring in *Epinephele wagneri* (fig. 149). The stripe becomes generally convex but in the posterior cells (1st, 2nd) the convexity is more pronounced than in the anterior ones with the exception of a very small piece in the 1st cell that forms a minute hook bent in the opposite direction along the 1st vein. The stripe somewhat resembles a hanging string fixed by its fore end and the said hook. Another specimen of *wagneri* (fig. 148) shows yet no hook, the general curvation, however, is already begun, and thus the transition from the prototypical status (fig. 147) evident enough.

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The next two modifications are hindwing replicas of the two already considered in the previous section and consist of general dislocations of the stripe. In fig. 151 (*Coenonympha oedippus*) M^1 and the ocellar series are in contact owing to the basifugal dislocation of the former. In fig. 150 the dislocation is less pronounced. The correspondence of the two figures to the respective forewing drawings (figs. 131, 132) is quite evident. The absence of the anterior portion of the Media observed both in figs. 150, 151 is not easily accounted for. It is possible that like forewing it has disappeared owing to the fusion with the 6th ocellar complex. Fig. 153 (*Satyrus saraswati*) shows a very typical charaxisation; the stripe has acquired straight form and therefore entered the discal cell. Fig. 152 (*Satyrus brahminus*) exhibits a transition from the prototype. It is out of doubt that the above modification and that already described in the forewings of the same specimens (figs. 133, 134) are in fact parts of a single process of basipetal dislocation.

The next forms of the first Media are all due to local dislocations. In fig. 155 (*Coenonympha corinna*) in the anterior part of M^1 there is a broad tongue-like protrusion. A similar though much smaller protrusion is seen in the 2nd cell. A transitionary condition from the prototype is to be seen in another specimen of the same species (fig. 154). The modification somewhat resembles one of the forewing ones, viz., that represented in fig. 136. In both cases the protrusion of M^1 is shaped tongue-like and located in the 4th and 5th cells. Such being the case we might number this modification among the bi-alar ones like the two preceding ones. An essential difference from the latter, however,

is that in the present case the two wings in question (fig. 136, 155) belong to different genera. This, however, is not a circumstance disproving the identity of modifications. We have seen already several examples when a given modification is existing only in the forewing of one species or genus and in the hindwing of another and nowhere in both wings of a single individual. This is the case of some third Externa forms (fig. 35) and af anti-erebisation of eye-spots (fig. 90).

Fig. 157 (*Satyrus fidia*) differs from the prototypical condition by a slight basifugal dislocation of the first Media along the 4th vein and by its basipetal shifting in the 2nd and also in the anterior cells particularly in the 6th one. The result is that the middle of the stripe forms a large though not sharp denticle the outline of which runs roughly parallel to that of the discal cell. Fig. 156 (the same species) is again intermediary between 147 and 157. The modification somewhat resembles that on the forewing represented in fig. 142. The main point of resemblance is the location of denticles in both cases on the 4th vein. This, however, is counterbalanced by the character of dislocations themselves. On the forewing the moving force is evidently directed exactly along the vein with the result that the stripe is tapering in the distal direction, and clearly distended. Nothing of this sort may be noticed in fig. 156, 157 where the denticles are rather blunt. Because the distension of stripes belongs to their most important properties its manifestation or non-manifestation is important and two modifications can be hardly classified together which differ from one another with regard to this.

In fig. 158 (*Aphantopus hyperanthus*) a tongue-like protrusion is observed resembling that of fig. 154 but situated in the 3rd and 4th cells instead of 4th and 5th. In fig. 159 (*Aphantopus arvensis*) the anterior part has become concave and the posterior roughly straight, the two being divided by the said protrusion. Besides this the area proximal to M^1 is melanised and the stripe has lost its strial character. It should be remarked here that similar shape of the first Media has been described in the Eastern Satyrid *Lethe* (B.N.S. & Sokolov, 1934, p. 164—165).

A very singular modification termed coenonymphoid is represented in fig. 161 (*Coenonympha thyrsis*). Its typical feature is that the portion of M^1 lying in the 3rd and 4th cells first approaches the discal veins (fig. 160) and then comes to lie within the discal cell (161), so that no trace of the stripe remains in the 3rd cell. In the preceding part of this work the gradual migration of the stripe in to discal cell is followed step by step (1935, p. 224, figs. 259—265) so that the remarkable process of a stripe passing over the vein during the dislocation is firmly established. The convex shape seen in all the cell-portions in figs. 160, 161 is not essential for the modification.

Finally the modification represented in figs. 162, 163 (*Coenonympha semenov*) undoubtedly belongs to the most singular ones. In fig. 162 M^1 forms

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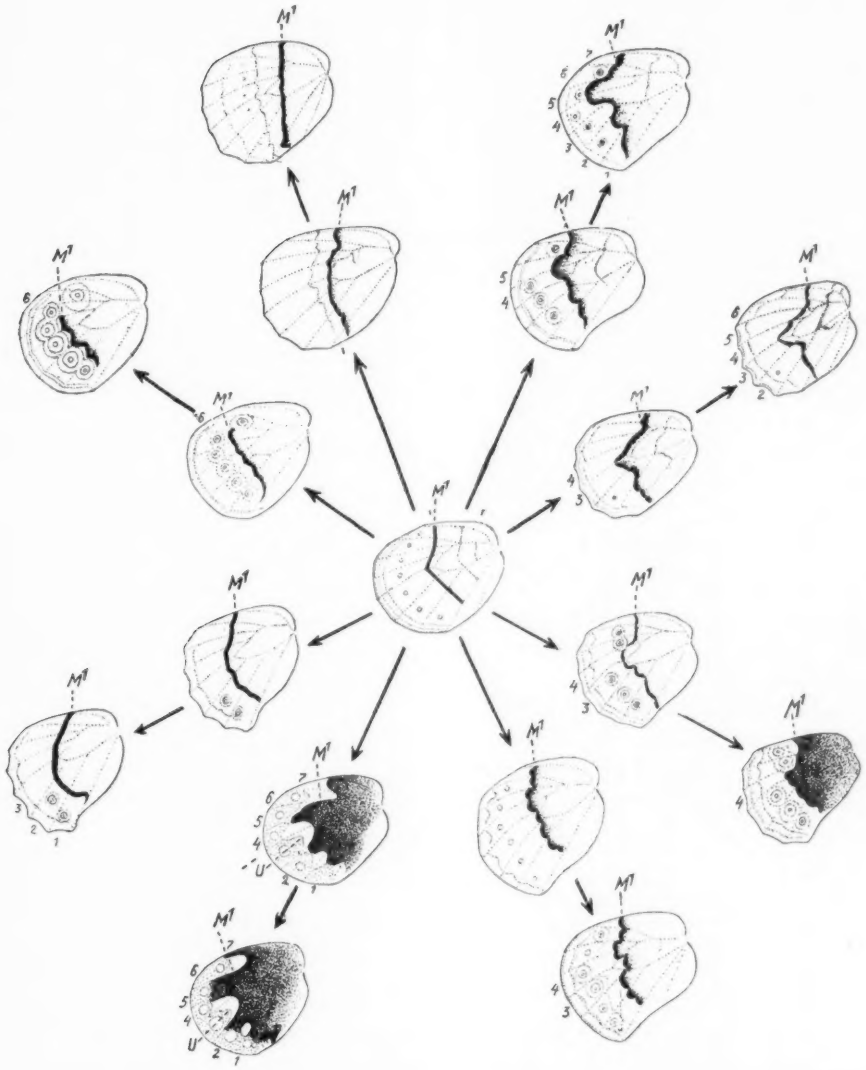


Figs. 147—163. Eight ways of polymorphic radiation in the hindwing first Media (M^1). Arrows show their directions. 147—prototypical condition; 148—149—a peculiar curved out shape (*Epinephele*); 150—151—approximation to ocellar series (*Coenonympha*); 152—153—charaxisation (peculiar basipetal shifting) in *Satyrus*; 154—155—tongue-shaped basifugal protrusion (*Coenonympha*); 156—157—denticle-shaped form (*Satyrus*); 158—159—curved in anterior part (*Aphantopus*); 160—161—coenonymphoid dislocation, i.e., M^1 enters the discal cell (*Coenonympha*); 162—several basifugal protrusions fused with *U* in 163 (*Coenonympha*). For species names see p. 60.

four large outgrowths placed in the 1st, 2nd, 4th and 7th cells. They show no contact with the Umbra (*U*) but in the final specimen (fig. 163) two wide Umbro-Medial coalescences develop in the 1st and 2nd cells a third which is the widest of all takes place in the 4th and 5th cells and one more very narrow fusion may be seen in the 7th cell. All of them represent further developments of the tongue-like outgrowths of fig. 163. It should be added that like several preceding cases M^1 has lost its strial character owing to a melanisation of the cis-Medial area. Some likeness of the modification to that represented in fig. 155 cannot be denied because of a similar location of the outgrowths in both. But in the general character they differ so much from one another that can be hardly classified together.

Thus it is evident that the diversity of the first Media forms of the hind-wing is but a little inferior to that of its forewing counterpart. We have also seen that only a few modifications are due to general processes affecting both wings equally.

There is only one modification for which parallel occurrence has been recorded. Series XVII shows that coenonymphoid form of M^1 is met with besides *Coenonympha* in two more genera. In *Satyrus* (fig. 172) its manifestation is quite typical, in *Pararge* (fig. 173) the stripe being typically bent in in the 4th cell does not enter the discal cell. Because the latter circumstance is due to the shortening of the cell itself while the curvation tendency influencing the stripe seems not to differ essentially from that of *Satyrus* and *Coenonympha* it is reasonable to include *Pararge* into series XVII.

5. SECOND MEDIA.

Second Media like the first one, is very liable to modifications, and though the latter are less numerous here their character is sometimes of great interest.

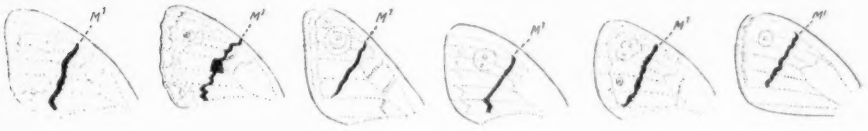
A. Basifugal dislocation and broadening.

In the prototype (fig. 175) the second Media (M^2) crosses the discal cell at a considerable distance from its closing veins. In fig. 175 a (*Melanargia titea*) the discal portion of M^2 is markedly bent out and the curved part of the stripe has approached the indicated veins.

Another modification is represented in fig. 176 (*Satyrus briseis*). The stripe retains its prototypical position but has markedly expanded and acquired the character of a blotch.

The two above modifications may be combined together as it is seen in fig. 177 (*Satyrus heidenreichi*) where the discal portion of M^2 has approached to the veins like fig. 175 a and is broadened and blackened no less than in fig. 176.

Thus two processes, viz., dislocation and broadening occurring either singly or both together result in three different patterns.



Series XV.

Figs. 164—169. Oblique position of M^1 in six genera.

Series XVI.

Figs. 170—171. Ladder-like (melanargoid) dislocation of M^1 in two genera.

Series XVII.

Figs. 172—174. Basipetal dislocation of M^1 in the 4th cell (coenonymphoid dislocation) in three genera. Letters and species names see pp. 3 and 60 resp.

Figs. 175—177. Three modifications of the discal portion of M^2. 175—prototypical condition; 175a—basifugal dislocation without widening (*Melanargia*); 176—widening without dislocation (*Satyrus*); 177—basifugal dislocation and widening (*Satyrus*). Lettering and species names see pp. 3 and 61 resp.

B. Pierellisation and triphysation.

Pierellisation (B.N.S. 1925) essentially consists of basipetal shifting of postdiscal portions of the Mediae which may become continuous with the discal portions of neighbouring components and thus give origin to complex stripes. The process occurs more often in the second Media than in the first one, and fig. 178 (*Pararge maera*) represents a good example of it on the forewing. The postdiscal portion of the second Media ($M^2 1$) has broken off from the discal one (M^2) and being placed on the level of D^2 forms a part of a complex stripe to be termed $M^2 1 + D^2$. Besides Pararge this modification occurs also in *Satyrus* (fig. 182 in series XVIII) where it is typically pronounced though without D^2 participation in the processes. Its initiation may be traced also in *Oeneis* (fig. 183).

Hindwing pierellisation generally belongs to unfrequent processes. Nevertheless rather an evident development of it is observed in *Melanargia* (fig. 179). Both first and second Mediae are divided into anterior ($M^1 a$, $M^2 a$) and postdiscal ($M^1 p$, $M^2 p$) portions the latter being shifted basipetally. The most interesting is that the crooked hind end of $M^2 a$ lies close by the fore end of

M^1p, and were the crook of the former straightened out M^1p and M^2a would be joined into a single complex stripe. The general shape of the latter is shown by my having drawn with black its constituent parts.

The last modification to be dealt with in the present section may be named triphysation. It consists of bilateral dislocation of the second Media along the existing or atrophying veins. The former case is seen in fig. 180 (*Satyrus huebneri*) where the stripe forms a typical projection markedly tapering towards the wing-base and evidently distended. As series XIX shows the process occurs in *Coenonympha* almost in the same form (fig. 187), while in *Epinephele* and *Triphysa* (figs. 186, 188 resp.) the dislocation is directed along an atrophied vein in the discal cell. A small supplementary denticle corresponding to the latter dislocation may be noticed also in *Coenonympha* (fig. 187).

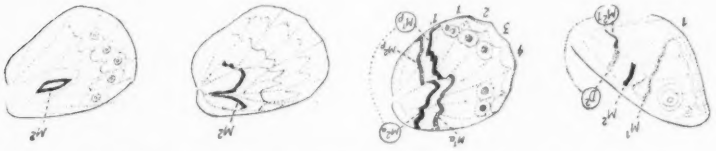
In *Triphysa* the dislocation results in a division of the stripe into two halves, the peripheric ends of which are also curved basipetally (fig. 188). The two ends of the hind half may meet one another and thus form an elongated ring as seen in fig. 181. This coalescence represents the ultimate result of the process named triphysation.

6. MEDIAL SYSTEM AS A SINGLE COMPONENT.

All the foregoing data concerning the evolution of the first and second Mediae do not show any dependence of the two components upon one another, with the exception perhaps of a single case, viz., that of pierellisation. But it is well established in my own and other writers' investigations that the Medial stripes represent a symmetrical system. It is natural that there are modifications illustrating the indicated circumstance. In the present work two kinds of such are expounded, viz., change of breadth and division of the Medial system.

A. Narrowing and broadening.

On comparing fig. 189 (*Melanargia titea*) with every of figs. 3—12 it is evident that M^1 and M^2 have considerably approached to one another as compared to their prototypical status. Just as opposite modification is seen in the next fig. 190 (*Erebia parmenio*) where the distance between M^1 and M^2 is apparently more than thrice as broad as in *Melanargia*. In both above forms the breadth of the interspace in question may be regarded as roughly uniform along all its extent, so that undoubtedly the whole of the Medial system is narrowed in *Melanargia* and broadened in *Erebia*. Different is the case of fig. 191 (*Erebia sibo*) where the system is hugely expanded in its middle cells, narrowed and even constricted near the hind end and shows more or less normal breadth in the anterior cells. Thus one could say that in *Erebia sibo*



Figs. 178—181. Modifications of M^2. 178—pierellisation, i.e., $M^2 1$ breaks off from M^2 and approaches to D^2 (*Parargе*); 179—pierellisation; $M^1 p$ has broken off from $M^1 a$ and approached $M^2 a$ (*Melanargia*); 180—triphysoid dislocation, i.e., M^2 is stretched along a nervure (*Triphysa*); 181—development of fig. 180 status results in a ring-shaped M^2 (*Triphysa*). Letters and species names see pp. 3 and 61 resp.

Series XVIII.

Figs. 182—184. Pierellisation of M^2 in three genera, i.e. $M^2 1$ is broken from the rest of M^2, shifted basipetally and (184) approached to D^2.

Series XIX.

Figs. 185—188. Triphysoid dislocation of M^2, i.e. basipetal distension along present or atrophied nervures, in three genera. Letters and species names see pp. 3 and 61 resp.

Figs. 189—191. Breadth of $M^1 M^2$ system. 189—narrowed (*Melanargia*); 190—broadened in the whole (*Erebia*); 191—broadened in the middle part only (*Erebia*). Letters and species names see pp. 3 and 61 resp.

a combination of narrowing and broadening of the Medial system is exemplified. It is evident that the essence of the above modifications consists of the change of breadth of the Medial system as a whole, and that the two stripes of the system so independent in the numerous examples dealt with in the foregoing sections are totally subordinated to some general principles in the three above modifications. This conclusion is totally supported by the fact that KÜHN and HENKE (1929—1936) have established the existence of two in-

dependent genes influencing the breadth of the Medial system in the Mediterranean flour moth *Ephestia kühniella*. One of them narrows another broadens the system when dominant.

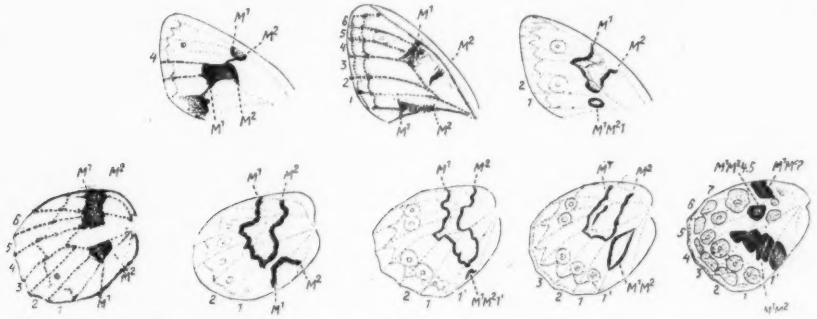
B. Divisions.

The unity of the Medial system is the most obvious when it undergoes transverse division thus behaving as a single broad component. The examples of this sort of processes are rather diverse and numerous in our nine genera. It should be reminded once more here that the patterns to be examined represent final members of morphological series each beginning with undivided condition the latter being described in the preceding parts of the present work (1929, 1931, 1935).

a. *Forewing.*

Let us begin with the forewing. In fig. 192 (*Melanargia lachesis*) M^1 and M^2 have very closely approached to the discal vein thus bringing about a very conspicuous constriction of the Medial system the latter remaining rather wide before the constricted area and considerably widened behind it. Thus no actual division takes place here but a very little remains to have it completed. Two more examples of the same constriction may be seen in the representatives of *Erebia* and *Triphysa* in the series XXI. Though in the latter the modification is far from being so pronounced as in *Melanargia,* it is nevertheless quite evident.

The next form of division stands somewhat apart from all the rest. Fig. 193 (*Satyrus arethusa*) exhibits its M^1 and M^2 consisting each of anterior and posterior parts divided from one another by a wide empty space in the 2nd and 3rd cells. As it is shown by the morphological analysis of this pattern (B.N.S. 1929) the disappearance of Mediae from the indicated cells is due to their atrophy in loco without any dislocations. This is in accordance with the fact that none of the four severed ends of the two stripes shows any approximation or inclination towards its neighbour, and thus evidently no constriction like that of the preceding case takes place in the present one. In spite of this it may be hardly doubted that some common factor has acted simultaneously on both Medial components and having deleted definite parts of them has caused the division of the Medial system as a whole. Two more examples belonging here are to be seen in the series XX. In a *Melanargia* (fig. 201) M^1 is nearly atrophied in the 2nd cell being sufficiently pronounced in the 1st and 3rd ones. In spite of the total absence of M^2 it is evident that the factor which suppresses M is located partly at least just as in *Satyrus arethusa*. A *Pararge* (fig. 202) shows a closer resemblance to the latter M^2 being also present. On the other hand, however, the hind ends of both M^1 and M^2 are



Figs. 192—199. Seven forms of interruption of M^1M^2 system. 192—constriction in discal and 4th cells (*Melanargia*); 193—disappearance of the most postdiscal portions (*Satyrus*); 194—breaking off of M^1M^21 portion (*Satyrus*); 195—interruption in the discal cell (*Satyrus*); 196—the same in the 1st cell (*Erebia*); 197—the same in the cell I' (*Melanargia*); 198—another form of interruption in the 1st cell (*Melanargia*); 199—two interruptions owing to division into M^1M^2, $M^1M^24.5$ and M^1M^27 (Pararge). Lettering and species names see pp. 3 and 61 resp.

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totally lost and the fact that M^1 is still existing in the 3rd cell resembles *Melanargia* and differs from the *Satyrus* condition. These distinctions are, however, not very important, and in general series XX demonstrates interruption of Mediae without constriction of the whole of the system.

The last example to be considered in this section is represented in fig. 194 (*Satyrus regeli*). The hind ends of the Medial system M^1M^21 represents a regularly shaped oval and as it is clear both from its origin described elsewhere (B.N.S. 1929, p. 600) and from the very shape of the two parts of it that the process leading to the figured final status represents a most typical constriction passing along the 2nd vein.

b. *Hindwing.*

There are five forms of division to be dealt with in this section.

In fig. 195 (*Satyrus briseis*) the line of division passes along the discal cell. The anterior half of the divided M^1M^2 shows all traces of constriction, viz., its posterior end is of a round shape and the dark area between M^1 and M^2 is surrounded with a black uninterrupted stripe thus evidently the "wound" being closed by two coalesced components. The posterior half is severed as it were, the fore ends of M^1 and M^2 show neither coalescence nor even mutual approximation, and thus "the wound is open". The morphological analysis of the case does not add anything essential to the above, and it seems not unlikely that the stripes are prevented from coalescence by the influence of the vein passing just along the severed edge. At any rate the case may be regarded as a most typical division caused by a not quite typical constriction.

But the division along the discal cell occurs in several more genera, and in some of them it is more typical than in *Satyrus*. Series XXII illustrates a

complete interruption of the Medial system in four genera, viz., *Satyrus, Oeneis, Melanargia* and *Pararge*, while in *Erebia* and *Coenonympha* the system is constricted at the discal veins, the constriction almost reaching its completion, i.e., division, in the latter genus, and pronounced though not much advanced in the former. Now the closing of the "wounds" caused by constriction is easy to see in *Oeneis, Melanargia* and also in *Pararge*, in all of them the dark areas of the Medial system are bordered by still darker margins obviously corresponding to curved and confluent M^1 and M^2. Thus it seems out of doubt that in these genera the division is due to constriction.

The next two forms of the division of the Medial system differ from the preceding one only by their location. The line of division passes along the 1st cell in fig. 196 (*Erebia gorge*) and along the cell 1' in fig. 197 (*Melanargia larissa*). The dependence of division upon constriction is too evident in both forms to discuss it. It should be only mentioned here that the 1st cell form of division also occurs in *Melanargia* as it is shown in series XXIII.

The next form of division to be seen in fig. 198 (*Melanargia arge*) is of a rather complicated sort. The M^1M^2 system is interrupted in the 1st cell. The spindle-shaped form of its posterior half does not represent anything exceptional. Some data expounded elsewhere (B.N.S. 1931, p. 349) lead to a conclusion that the Medial system is also divided in the cell 1' in a manner like that of fig. 197, but the posterior small portion has disappeared and thus the Medial system of *Melanargia larissa* should be regarded as having undergone two divisions, i.e., one in the 1st cell and another in the cell 1'.

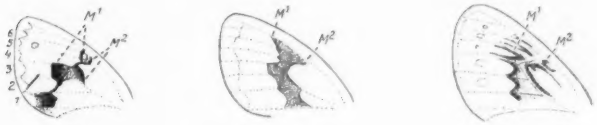
An undoubted division into three parts (M^1M^2, $M^1M^2{}_4{}_5$, $M^1M^2{}_7$) is represented in fig. 199 (*Pararge thibetana*) which, however, should be derived not from the above *Melanargia* status (fig. 198) but from that of *Satyrus* (fig. 195) by a division of its anterior M^1M^2 half into two more halves.

The data given in the two foregoing sections show clearly that both on fore and hind wings the Medial system is liable to divisions on different levels, the process may occur twice in the same wing, and the cause of it is mostly constriction. In all these modifications M^1 and M^2 together with the interspace lying between them behave as a single broad stripe.

Now just as it has been pointed out in the description of E^3 forms, the interruption of the Medial band may be regarded as an example of polymorphic radiation on the one hand and as that of "intercomponential parallelism" on the other. The former contention hardly needs to be argued. It is selfevident that the forms of the M^1M^2 band represented in figs. 192—199 differ from one another, and consequently the directions of their evolution are also different this being the essence of polymorphosis. But on the other hand they are all due to division, and in this principal fact they are all alike. From this point of view the existing differences depend mainly upon those in the loci of the

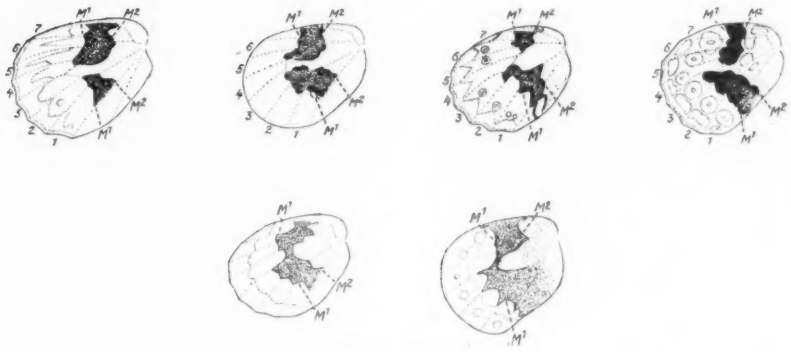
Series XX.

Figs. 200—202. Atrophy of postdiscal portions of M^1 and M^2 in three genera.



Series XXI.

Figs. 203—205. Constriction of M^1M^2 in the 4th and discal cells in three genera. Letters and species names see pp. 3 and 61 resp.



Series XXII.

Figs. 206—211. Interruption or constriction of M^1M^2 system at the discal cell level in six genera.

Series XXIII.

Figs. 212—213. Interruption of M^1M^2 system in the 1st cell in two genera. Lettering and species names see pp. 3 and 61 resp.

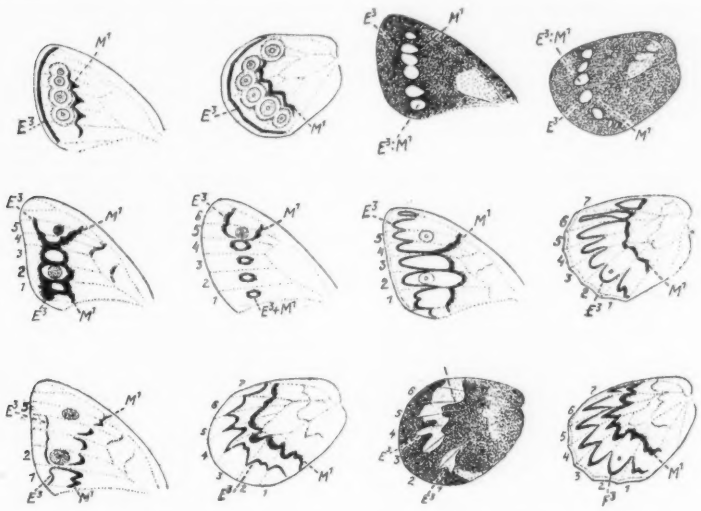
process. If the dividing force may be directed in the hindwings along the 6th cell, or 4th, or 1st, or 1' it becomes clear that the phenomenon may be considered as a sort of parallelism differing from its common form in the fact that a given modification is met with not in different genera or families but in different parts of a given component. It does not matter what are the systematic positions of the individual beareres of the modification in question. The "intra-componential" parallelism may exist even in a single organism. The two interruption of M^1M^2 system in *Pararge* (fig. 199) illustrate this phenomenon as well as a comparison of figs. 195 (*Satyrus*) and 196 (*Erebia*). On the other hand though the wing of a butterfly does not represent a metameric organ, the serial sequence of cells and pattern components is somewhat related to serial homologies of segmented animals.

7. MEDIO-EXTERNAL COALESCENCES.

If in the preceding section correlative modifications of the components belonging to the same system have been described, in the present one we have to deal with several forms of the fusion of the first Media and third Externa with each other which stripes belong not only to different systems but are moreover divided by a third one, i.e., the ocellar series. In spite of the latter circumstance the respective tendency is very strong and there are several ways by which the fusion is fulfilled.

The first modification to be considered here is the basifugal dislocation of the first Media in *Coenonympha* already described in the foregoing. In figs. 214, 215 a denticulated M^1 and the components of the ocellar series are put in contact. Were this modification be alone in existence one could hardly deduce anything from it, but having in view the subsequent data the suggestion seems most natural that M^1 in its dislocation towards E^3 is stopped by the ocellar series. If so a far reaching fusion of M^1 with E^3 should be expected when the eye-spots are absent. This is really so. In figs. 216, 217 (*Erebia pawlowskyi*) there is no eye-spots at all, and it is ready to see that E^3 and M^1 though representing but boundaries of adjacent dark areas have closely approached to each other and have either fused along most of the veins or show a strong tendency to do so. The interspace $E^3 : M^1$ between the two stripes has thus dissolved into a series of oval markings. Gradual development of the process is described elsewhere (B.N.S., 1935, p. 199), and it should be remarked that the process of fusion may develop further especially on the hindwing with the resultant total disappearance of the remainders of the $E^3 : M^1$ interspace.

A very interesting detalisation of the above interdependence may be seen in figs. 218, 219 (*Satyrus bischoffi* and *Satyrus palaearcticus*). In *bischoffi* the eye-spots are retained in the 2nd and 5th cells, in *palaearcticus* the only eye-



Figs. 214—225. Nine cases of approximation and coalescence of E^3 and M^1. 214—215—dislocation of M^1 towards E^3 is hindered by ocellar series (*Coenonympha*); 216—217—E^3 and M^1 approach one another and coalesce on the nervures (*Erebia*); 218—219—two more forms of the same phenomenon in *Satyrus*; 220—221—E^3 and M^1 are stationary, their coalescence is due to E^3 stretching along the veins (*Satyrus*); 222—E^3 and M^1 are nearly stationary, coalescence in 1st cell is due to M^1 stretching along 2nd vein (*Satyrus*); 223—interveinous approximation of M^1 and E^3 towards one another (*Erebia*); 224—interveinous coalescence of M^1 and E^3 in the 2nd cell (*Erebia*); 225—denticles in E^3 are veinous basipetal, in M^1 interveinous basifugal, no fusion is likely (*Satyrus*). Letters and species names see pp. 3 and 61 resp.

spot present is in the 5th cell. In both species M^1 and E^3 show veinous fusions in the middle and posterior areas of the wing while in the anterior one the stripes diverge widely. The most interesting distinction of *palaearcticus* from *bischoffi* is that in the former the fused stripes have dislocated considerably towards one another with the result that the E^3+M^1 rings have become small. This may be ascribed to the absence of any hindrances in the way of dislocations. Different is the case of *bischoffi* where the large 2nd eye-spot keeps as it were the coalesced stripes away from one another, and the ovals so small in fig. 219 are much larger in fig. 218, the largest being that in the 2nd cell. Thus forms of E^3+M^1 fusion seem to depend upon eye-spots. The latter if numerous may totally prevent it (figs. 214, 215), if few—modify it (figs. 218, 219) and if absent (figs. 216, 217 and hind cells in fig. 219)—the fusion becomes very full.

All the above examples of E^3+M^1 fusion consist of a more or less general dislocation of the stripes. The case is different in several forms to be considered next.

In figs. 220, 221 (*Satyrus pricuri*) E^3 forms a series of veinous denticles. Some of the latter are so long that their proximal apices are fused witht M^1.

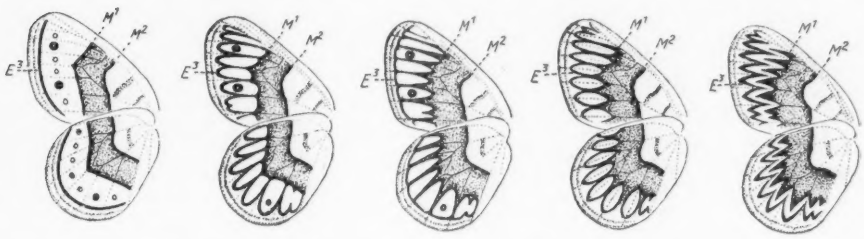
This is the case in the middle area of fig. 220 and in the anterior one of fig. 221. The elongation of the E^3 cell-portions is extreme while M^1 remains unchanged. On the other hand the interveinous points of E^3 show but a slight basipetal dislocation so that with the exception of denticles the stripe may be considered as almost stationary. Therefore the cellular interspaces between the fused E^3 and M^1 are very much elongated (2nd and 3rd in fig. 220, 6th in fig. 221).

Another form of the "fusion of stationary stripes" is represented in fig. 222 (*Satyrus fatua*). It is easily seen that in its 1st cell M^1 emits a long tapering prolongation running along the 2nd vein towards E^3 and fusing with it. The shape of E^3 in the 1st cell suggests no idea of its bending towards M^1. Similarly in the anterior cells E^3 is straight while the cellportions of M^1 though not reaching E^3 are nevertheless clearly curved basifugally along the nervures. The general position of M^1 in fig. 222 is, however, but slightly deviating from the prototypical one, so that contrary to the preceding case the fusion of the generally stationary E^3 and M^1 is due to the latter's veinous elongations.

In fig. 223 (*Erebia ocnus*) the E^3 cell-portions are very markedly bent in, while those of M^1 form distally distended tongues in most of the cells. The result is that in the 3rd and 4th cells the stripes lie very close by, though show no contact. Similar modification in fig. 224 (*Erebia cyclopius*) results in an actual coalescence of the two stripes in the 2nd cell and in their close contact in the 1st one. The fact that both components represent boundaries of dark areas is of secondary importance. This example of fusion is just as opposite to the preceding ones, since in all of them (figs. 216—222) the stripes coalesce on the veins, while the *cyclopius* form of coalescence should be termed interveinous, as the stripes fuse along the bisecting lines of the cells.

A very curious result of two "non adjusted" processes may be seen fig. 225 (*Satyrus geyeri*). Its E^3 cell-portions are convex and the apices of proximally turned denticles lie on the veins. The M^1 cell-portions are also convex and the distal ends of their denticles are located between the veins. The result is that the denticles of two stripes though turned towards each other are alternating and therefore no contact takes place inspite of their very close position, e.g., in the 5th and 6th cells. Were the M^1 distal denticles veinous or the E^3 proximal ones interveinous, a far reaching fusion would be undoubtedly existent. Because, however, the modifications of the two components are "wrongly" combined no coalescence takes place.

The process represented in figs. 220—225 differs from that illustrated by figs. 214—219 in two respects. First the fusing stripes may be regarded as more or less stationary the actual fusion being that of their long outgrowths which is not the case of figs. 214—219 with their totally moving stripes. Hence the shape of the interspaces between E^3 and M^1 becomes oval or almost circular in the latter group of wing-patterns and very elongated in the former. Second



Figs. 226—230. Diagrams of the fusion of stationary E^3 and M^1. 226—prototypical status; 227—veinous fusion due to E^3 being elongated on nervures; 228—the same due to respective M^1 elongations; 229—interveinous fusion; 230—basipetal veinous E^3 denticles and basifugal interveinous M^1 ones are unfavourable for a fusion. Letters see p. 3.

the eye-spots seem to influence the extent of the fusion of the dislocating stripes, while no influence of this sort may be recorded in the other form of fusion. It is especially well to see in fig. 220.

The four described forms of "stationary coalescence" may be recapitulated by means of diagrams (figs. 226—230). We have seen that in real patterns a given coalescence takes place either in a few cells (figs. 220, 221) or even in a single one (figs. 222, 224). The essence of the diagrams is that every form of fusion is attributed to all the cells of both wings—a status very unlikely to be ever discovered in Nature—but showing respective tendencies in a much clearer form than the actual phenomena. Fig. 226 represents the prototypical status of E^3 and M^1, the interspaces between them being wide and uninterrupted. The next two diagrams show veinous fusions. In fig. 227 E^3 emits protrusions while M^1 is unmodified, in fig. 228 on the contrary E^3 is unmodified while protrusions are formed by M^1. The real foundations of these diagrams are figs. 220, 221 and 222 resp. In the next diagram (fig. 229) the interveinous fusion is represented that has been met with in *Erebia* (fig. 224). And finally fig. 230 shows absence of fusion due to the "wrong orientation" of strong protrusions of both stripes in question. The diagram is based on *Satyrus geyeri* (fig. 225).

8. UPPERSIDE.

It seems that the most prototypical forms of the upperside pattern are those which reproduce more or less wholly the respective undersides on condition, however, the latter being themselves prototypical enough. A few examples of this sort are dealt with in the preceding parts of this work (1929, 1931, 1935) but they do not interest us here. A very widespread way of the upperside evolution consists of the melanisation of definite interspaces so that they become as dark as the bordering stripes, and thus the latter lose their strial character. Generally the process starts with a few interspaces, then it affects more and

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more of them and leads to a complete melanisation of wings and suppression of pattern. But on the other hand some components may disappear before the beginning of melanisation and thus the spreading of the latter be restricted to a very few areas.

Figs. 231—252 (series XXIV—XXIX) represent on the one hand six apparently principal types of the upperside patterns of palaearctic Satyrids, and on the other their parallel occurrence. Two remarks should be made before to examine them. First of them is that only five genera out of nine are included in the table. Generally *Triphysa* and *Aphantopus* show nothing in particular which is natural as they are very small. Genus *Coenonympha* in spite of a great scale of its underside evolution does not afford anything of much interest for the upperside analysis. Finally the uppersides of *Melanargia* are very interesting and dealt with by me elsewhere (1931) but the direction of their evolution is so widely deviating from the remaining genera of the group that almost no comparative material may be drawn from them. Another remark is that to make the comparisons easier some of the figures are more darkened than others as compared to the real patterns. This is especially the case of figs. 240, 242.

A salient feature of the upperside to be named External consists of the melanisation of the narrow interspace distal to the third Externa or trans-External area (tE^3 in figs. 231—235). This modification is markedly pronounced in both wings of the four genera placed first in the series XXIV and in the forewing of *Erebia*. The rest of the wings shows in all the genera numerous (*Oeneis*) or few eye-spots and in some of them also remainders of M^1 (*Satyrus*), D^1 (*Satyrus, Pararge, Erebia*) and of U (*Pararge*). They, however, play but a subordinate rôle and all the uppersides of XXIV series, with the exception of *Erebia*, may be described as generally light. Their actual hues are more or less yellowish. *Erebia* is of course much deviating form the other four owing to its hindwing being totally melanised. In the forewing, however, melanisation is restricted to the dorsal area so that in general this wing may be rather rightly included into the series.

In series XXV trans-External melanisation is supplemented by that of the interspace between M^1 and M^2. *Erebia maurisius* (fig. 238) shows the modification in its purest form, in *Satyrus abramovi* (fig. 236) melanisation of the Medial system is not completed yet. Presence of eye-spots or their absence (*Satyrus* and *Erebia* resp.) is unimportant. *Pararge dumetorum* (fig. 237) though showing a very far reaching melanisation is nevertheless included into series XXV because of its Medial system being still visible on the forewing as individualised component that not being the case in any of the subsequent uppersides.

Series XXVI represents Medio-External type of upperside. Were the whole of the area proximal to M^1 in fig. 236 to be totally melanised a condition almost exactly like that of fig. 239 would be brought about. The wide light area seen

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Series XXIV—XXIX.

Figs. 231—252. Parallelism in the gradual melanisation of the upperside. XXIV—melanisation of trans-Externa zone (tE^3) in five genera; XXV—melanisation of M^1M^2 zone in three genera; XXVI—melanisation of cis-M^1 zone in five genera, E^3:M^1 interspace being left light (Medio-External pattern); XXVII—U present on hindwing in two genera (Umbro-Medial pattern), forewing as in XXVI; XXVIII—U present on both wings, in three genera; XXIX—general melanisation except eye-spots and surrounding rings in four genera. Letters and species names see pp. 3 and 61 resp.

in all the patterns of series XXVI represents, as careful analyses published elsewhere (B.N.S. 1929, 1935) show, the interspace between the third Externa and first Media or Medio-External interspace ($E^3 : M^1$). But in the series XXVII the distal border of the light band is formed on the hindwing by the Umbra (U), the band thus becoming Umbro-Medial ($U : M^1$), while the third Externa, as the comparison to the underside shows (B.N.S. 1929, p. 613) is located in *Satyrus circe* (fig. 244) more distally and rendered invisible by the melanisation spread over it. The forewing of *Epinephele janira* (fig. 245) differs likewise from its hindwing, though the latter is less typical that in *Satyrus circe* as the Umbra fills up a considerable proportion of the $U : M^1$ area.

The Umbro-Medial pattern restricted to the hindwing only in series XXVII may spread on the forewing too. Though the hindwing of *Pararge deidamia* (fig. 247) represents again a much more advanced stage of melanisation all the remaining five wings of series XXVIII are Umbro-Medial ($U : M^1$). A typical feature of the Umbra in general, viz., dilution of its outlines is readily seen at the distal borders of all the interspaces in question. It differs markedly from the sharp borders formed by M^1 or in series XXVI by E^3. The reappearance of E^3 in *Epinephele* due to comparatively slight melanisation is unimportant for the above homologisation.

Finally nothing of the interspaces dealt with in the foregoing is left in the four forms composing series XXIX. In *Satyrus, Epinephele* and *Erebia* representatives the hindwings are totally melanised and show no pattern at all. In *Pararge* three eye-spots are existing in it still. Forewings show more uniformity exhibiting each the 5th eye-spot supplemented by the 4th one in *Erebia*. All the eye-spots are typically formed and show bright pupils in their centres. Each of them is surrounded by yellowish light zone which represents, as it is shown elsewhere (B.N.S. 1935, p. 168), the interspace between the eye-spot and encircling Umbra, and is termed intra-Umbral ring.

Melanisation may develop still further. A remarkable *Erebia manto* is totally melanised and shows no pattern at all on any of its eight wing-surfaces (B.N.S. 1935, p. 207). But it seems unnecessary to consider here the like forms as the general tendencies of the upperside evolution are made sufficiently evident in the foregoing description. We have seen that gradual melanisation advances step by step along a definite direction, so that all the first members of the series XXIV—XXIX, i.e., the species of *Satyrus* may be regarded as illustrating a single morphological process, and it is very interesting to emphasize that every step of the latter occurs in several genera.

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CHAPTER III.

RADIATING AND PARALLEL EVOLUTION.

1. SOME INTRODUCTORY REMARKS.

Evolution of organisms is an enormously complicated process. To establish the interrelations between the existing forms by a comparative way is only a fraction of the general problem of evolution. The wing-pattern of butterflies and moths serves an excellent basis for the work in this direction. In my previous publications several "rules" of pattern evolution have been formulated like the elimination of components, their dislocations of different sorts, formation of complex components and so on. It cannot be said, at least at present, that they are not right. Most of them represent effective tools in the pattern analysis. But they do not pretend to solve the problem of morphological diversity. An attempt to trace in the latter some rules of a more general character is made in the present paper. All the data dealt with in the two preceding chapters tend to illustrate two principles, termed polymorphic radiation and parallelism. It may be hardly doubted that they do not cut the matter very deep, but at the present time they seem to be the most general ideas which may be fished out of the material afforded by the nine genera of palaearctic Satyrids. If on the other hand none of them is new it should be remarked that nobody has studied systematically their manifestations in the wing-patterns of Lepidoptera.

Before passing on to these principles let us dwell for a time on a few other concepts necessary for the correct elucidation of the former.

Morphological and subsequent experimental analysis of the wing-pattern is wholly based on the idea of morphological units. The German writing authors often say (HENKE 1932, KOEHLER u. FELDOTTO 1935, HENKE 1935) that the new period in the study of wing-patterns began after the present writer in 1924 and SÜFFERT in 1926 had independently proved the existence of systems in the wing-pattern. This formulation being correct is, however, not quite satisfactory. The main generalisation made is that the colour pattern consists of a definite number of morphological units, or components, differing from one another in quality. From this principal fact the grouping of units into systems follows as a next step of generalisation. There is still a third one not stressed enough, viz., that all the systems are subordinated to the whole of the pattern.

Now what is a fundamental morphological unit? (If the gene may be generally regarded as indivisible elementary unit of hereditary mechanism there is nothing so exact in the morphology of wing-pattern.) Neither stripes are

elementary units as they often dissolve into minor parts mostly cell-portions, nor even the latter are such, as they may though seldom divide in their turn into still smaller particles, the number and character of which vary greatly, so that apparently no general rule may be established. Even the eye-spots which are generally very well individualised may undergo divisions. Nevertheless both the individual properties of parts which we name pattern components and their independence from one another are evident and they may be rightly regarded as organismal units or components though one might hardly name them elements. The word character is very largely in use but its meaning is very wide on the one hand and does not quite suit the purpose on the other. Almost every distinction of a given organism in its physiological activities, ecological dependences and so on may be very fittingly termed by this word. By morphological characters principally either presence or absence of a given part of the organism is meant or some features of that part or parts. E.g. presence of intestine in a trematode or its absence in a tapeworm are morphological characters of the respective groups. The length of the intestine in herbivores and its shortness in carnivores are again morphological characters. But the intestine itself irrespective of its special type cannot be termed a character. It is an organ even a system. Similarly presence or absence of the first Media or its oblique and ladder-shaped forms are undoubtedly characters. But the first Media itself may be hardly termed a character. One might perhaps name it organ, especially as the pattern represents a coordinated system. Because, however, functions are the most typical properties of organs, while at least at present no immediate function is ascribed to any part of the wing-pattern, it seems better to stick to the word component which though being somewhat too general is, however, exact enough and shows clearly that a part of something else is meant by it.

2. POLYMORPHIC RADIATION.

It is out of doubt that the fundamental way of the evolution of pattern components is that of their polymorphic radiation. We have seen in all the components dealt with in the foregoing their basic property to evoluate in different directions with the result that some final forms appear which are more or less widely differing both from one another and from the prototypical status, and we have accepted the term of polymorphic radiation for this sort of evolution.

Is it possible to imagine a considerable evolutionary process without participation of polymorphic radiation? Leaving parallel evolution temporarily out of consideration there is only one more way possible. Supposing a number of prototypical components to undergo elimination and the combination of

eliminated parts to be different, a considerable number of patterns may be thus obtained. The principle of combination is undoubtedly one of the most important ones in the evolution of wing-pattern, and its manifestations are many in the preceding chapters. Elimination of the second Externa, of definite eye-spots, of the second Media of both wings, or of both Mediae form the forewing—all these are examples of combination. It is easy to show, however, that were the evolution be governed by this principle alone the results would be but poor.

If in a component or in its part alterations of size, shape or position take place that would already belong to the domain of polymorphic radiation. Combination in its pure form may deal only with the presence and absence of prototypical pattern components. If even rather a great number of patterns be evolved by this negative process they all should be very uniform and monotonous and nothing that would resemble the existing diversity may be brought about. Thus no considerable efficiency may be expected from the principle of pure combination.

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Let us now consider polymorphic radiation somewhat closer. The instances of it given in the two preceding chapters are numerous. The fact is that, e.g., the first Media may undergo several sorts of dislocations, curvations and divisions and thus influence largely the general character of the patterns resulted in. The impression is born out as if the first Media is made of some plastic material that may be shaped and reshaped in a great many ways. The same comparison suits the evolution of all the remaining stripes though they are inferior in their plasticity to the first Media. Even the ocellar series taken as a whole behaves like a stripe and shows several ways of curvation (erebisation, anti-erebisation on forewings, on hindwings) but besides this several ways of the expansion of individual eye-spots have been noticed. The above consideration tends to express the very essence of polymorphic radiation. The latter undoubtedly represents a fundamental and positive way of evolution as there is a new form of component in every "radius" which exists neither in the prototype nor in any other part of the radiation scheme.

If, however, polymorphic radiation represents a fundamental way of the evolution of single components it cannot be solely responsible for the whole of the existing diversity of patterns. We have recorded three modifications in the second Externa, six of them in the third one and some eight in the ocellar series. As to the first Media there are ten modifications of its general shape on the forewing and eight on the hind one, the total being eighteen. Five modifications of its cell-portions should be added to them. The second Media yields some seven forms, the correlated modifications of both Mediae are eleven and finally there are eight ways by which first Media tends to fuse with the third Externa. Thus the number of the modifications of polymorphosis type is:

Second Externa	2
Third Externa	6
Eye-spots	8
First Media	18
First Media cell-portions	5
Second Media	7
Both Mediae	11
Third Externa and first Media	8
Total	65

There are some other modifications of the same components in palaearctic Satyridae which are not included into the above but they are few, and the obtained number 65 undoubtedly covers the great proportion of the modifications of single components. On the other hand the above calculation is somewhat "liberal" as some of the indicated modifications are the same on both wings. If the modifications are counted from this stricter point of view the total will be 59. Meanwhile the number of species and forms belonging to our nine genera according to the comparatively old SEITZ's data is 202 and 695 resp. but judging, e.g., by the new WARREN's *Erebia* monograph (1936) it should be much higher. Most of them have their own typical colour patterns differing from those of other species or forms. Because the differences in the appearance of butterflies, especially in closely allied species, are largely due to their color patterns, it is not a great overestimation to say that the two hundred of species and some seven hundred of forms of palaearctic Satyrids have as much wing-patterns. It is evident that the number of modifications of single components recorded in the group is far inferior to the number of existing patterns, and consequently the principle of polymorphic radiation in spite of its importance is not adequate to base upon it alone the existing morphological diversity.

3. PARALLELISM.

Here we come in touch with another principle that of parallel evolution, or parallelism. We have seen in the chapters II and III that if some of the modifications recorded occur but once, i.e., in a single genus and even species, there are many of them which occur in several genera and this fact serves a basis of our twenty nine parallel series. The essence of the thing seems to be quite simple. A given form of component, say an oblique first Media (series XV, p. 31) or concave cell-portions of the third Externa (series IV, p. 10) occur the former in six genera and the latter in eight of them. The phenomenon is well known and noted still by CHARLES DARWIN. Later on it has been dealt with by SCHIMKEWITSCH in Pantopods (1906), by ELTRINGHAM in Heliconid butterflies (1916) by ZAWARZIN (1925) in histological structures and by many

other authors in very different groups. VAVILOV (1920, 1922) described its general idea as "the law of homologus series". On the basis of the latter he predicted the existence of some forms of cereals discovered later on. The discussion of parallelism by KRENKE (1935) and also ROEMER's (1936) and KLEINSCHMIDT's (1936) papers should be also referred to.

The term of parallelism is figurative of course, but essentially the occurrence of a given modification in two or more morphological milieux may be meant by it. This definition requires some explanatory remarks. It is easy to see that all the parallel series dealt with in the foregoing are those of modifications. In none of them prototypical conditions are represented. This is made intentionally. By no means the nine generic patterns (figs. 4—12) may be regarded as examples of parallelism. They are all prototypes of the respective genera from which the evolution starts. The emphasis should be laid upon the fact that parallelism means parallel evolution, and the resemblances meant by it do not appear at the beginning of processes but only in their more or less advanced stages, like, e.g., curvation of E^3 cell-portions arises in several genera starting, from the prototypical rectilinear condition in every of them. If on the other hand some status is discovered in several processes before they develop more or less considerably, it is a definite indication on the prototypical nature of that status. Consequently resemblances are prototypical if they exist before the evolution begins and parallel if they appear after the beginning of the process.

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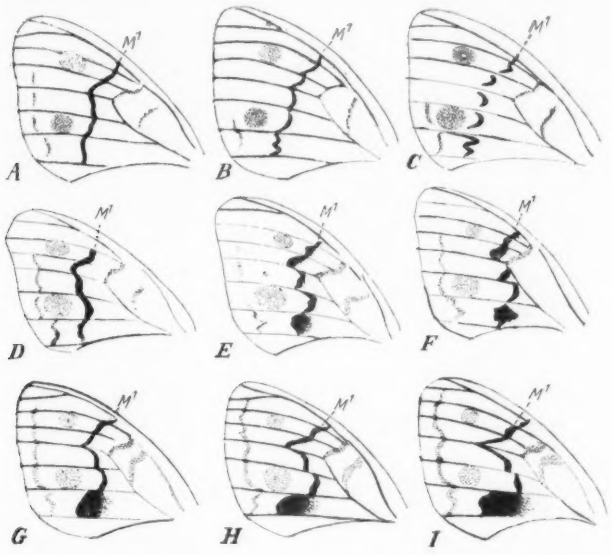
But in a research like this where different stages of processes represent in fact but members of variation series, and there is no real sequence in time one may be questioned how to distinguish the beginning of the evolutionary process from its end, or in other words how to identify the direction of evolution in a morphological series? The phenomenon of polymorphic radiation affords a sure means to answer the question. In figs. 253—261 a more detailed derivation of some three modifications of the first Media of *Satyrus* is given than that described in the chapter II (cf. figs. 141—146). Each horizontal series consists of forms belonging to the same species. The first vertical series (figs. 253, 256, 259) shows almost identical shape and position of M^1 in all the three species. The next vertical row is transitionary, in the last one M^1 exhibits three forms widely differing from one another (figs. 255, 258, 261). Thus the left ends of horizontal series are alike the right ones are not. Because the whole of almost ninety years' experience leads uniformly to the conclusion that evolution proceeds from general to special, it becomes evident that our three series begin at their left ends while the final conditions are at the right ones. Some two hundred morphological series described in my previous papers and some more unpublished ones show all the same: the condition at one end of a given series closely resembles those occurring in many others, the condition at another end cannot be discovered anywhere else. This circumstance leaves

no doubt as to how the series should be orientated, and as far as my experience goes the correctness of the polymorphic radiation concept is invariably corroborated by every new example of pattern analysis. Still another means to discern prototypical condition from a modified one lies in the fact that from the former several evolutionary directions always begin, while from the latter only one, i.e. that directed back to the prototype, may be traced. If the comparative material is ample enough this direction is always evident and the connection of a couple of modifications with each other may be established only "via prototype". As far as parallel resemblances differ in principle from the prototypical ones being due to modifying processes it is ready to see that the introduction of the term modification in our definition of parallelism is justified.

Now the definition of parallelism contains the term of morphological milieu or environment. Every of the parallel series I—XXIX illustrates the occurrence of a certain modification in several genera. Thus the members of a given series are all alike or even identical with regard to the modifications in question. For instance in the series IV (p. 10) the concave shape of the third Externa cell portions is essentially the same in all the seven represented specimens. It is no less evident that the latter so differ from one another in a great many characters that they are classifieed under seven different genera. Were it otherwise the specimens would be quite or very alike and no palpable manifestation of parallelism be existent. The structure of a parallel series may be represented as $pa^1b^1c^1d^1e^1$, $pa^2b^2c^2d^2e^2$, $pa^3b^3c^3d^3e^3$, $pa^4b^4c^4d^4e^4$, ... $pa^nb^nc^nd^ne^n$ where p stands for the component undergone a parallel modification and *abcd* for the remaining components that have undergone different modifications 1 2 3 ... n. the *abcde* part of the formulae may be named morphological milieu or morphological environment with regard to the component p. Were all the remaining components $a\ b\ c$ ... be in unmodified condition, all the members of the series would be identical and undistinguishable and no parallelism be in existence. It is of course unnecessary that every of the environmental components would be modified, since if some of them remain in prototypical status it does not interfere with parallelism, so that its representation as $pab^1c^1d^1e^1$, $pa^2bc^2d^2e^2$, $pa^3b^3cd^3e^3$ and so on is quite lawful. Of course the classification of components into environmental and parallel is conditioned. Every parallel character represents in its turn an integral part of the environment with regard to another character, and the latter may prove to be parallel if other species or genera are taken into consideration. These are all however things of secondary importance and the principal aim of their being discussed here is to justify and illustrate the thesis that without differences in "non-parallel" characters, in the "milieu", no parallelism at all may be demonstrated. If so the second part of our definition of the phenomenon is justified.

The foregoing description and discussion of parallelism are based almost



Figs. 253—261. Direction of the evolution of the first Media (M^1) in Satyrus. In *S. fatua* Frr. continuous (253) and perforated (255) forms of M^1 are connected by intermediary one (254); in *S. bishoffi* HS. continuous (256) and interrupted (258) forms of M^1 are connected by ladder-like one (257); in *S. anthe* O. continuous moderately curved (259) and interrupted denticle-shaped (261) forms of M^1 are connected by intermediary one (260). Three forms of M^1 of the right vertical column of figures differ considerably from one another, those of the left column are very similar. Because the evolution generally develops from general to special it is evident that the left and right columns represent prototypical and specialized conditions resp. and consequently the direction of the process in the diagram is from left to right.

Figs. 262—263. Diagrammatic representation of polymorphic radiation and parallelism. 262—polymorphic radiation without parallelism; 263—polymorphich radiation and parallelism. For full explanation see text p. 56.

wholly on one of its forms that may be called intergeneric, as in all the examples of the phenomenon comparisons of different genera are dealt with. One could easily multiply the examples were species taken instead of genera. This way is, however, intentionally avoided in the present work as though affording a much greater amount of facts it would add nothing to the elucidation of the principal idea or even would make it less evident. It is obvious that the greater is the difference of two morphological environments the more striking are the features which they have in common. Genera differ from one

another much more than species do, and hence intergeneric parallelism is more showy than interspecific one. Still more so would be parallel occurrences in different families. Their existence is beyond of any doubt. Such modifications as concave cell-portions of E^3, oblique position of the forewing M^1, pierellisation of M^2 and some others occur in a number of Nymphalid genera of both hemispheres, to say nothing of the exotic Satyridae. But this material is out of the scope of the present paper, though its special study would be of a great interest.

In the foregoing description we have met with a category of facts which though not numerous deserve, however, some comment. If the cell-portions of two stripes become convex it not of prime importance whether they represent e.g. E^3 of two individuals or E^3 and M^1 of a single one. It is most likely that there is some developmental factor which moulds the prototypical stripes as to bend their cell-portions into convex shape, and the two above examples differ only in the fact that the indicated factor is differently directed—i.e. to the same component in the case of typical intergeneric parallelism and to different components in the case of what may be named intercomponental parallelism. The latter phenomenon has been also recorded in the Lycaenidae, and it is shown in a paper prepared for press that if affecting a considerable number of components this sort of modification may lead to homomorphism. A popular example of the latter represent e.g. some *Argynnis* species with most of their stripes fragmentated into a number of similar round-shaped cell-portions. Similar, though less typical, is the case of *Pararge thibetana* (fig. 199).

4. ANTIMERISM.

We have now to consider the facts of antimerism mentioned repeatedly in the foregoing chapters. Perhaps there are two main forms of it. In one of them to be named unicomponental a given component is modified in two opposite directions thus rendering the forms resulted in to be mirror images of one another. Six forms of the third Externa cell-portions (figs. 31—36, p. 9), three of them being concave and three convex, serve one of the best illustrations of this sort of modification. Similar interrelations exist in the ocellar series (figs. 88—89, p. 17) and in the first Media (figs. 105—111, p. 21). It has been indicated already that such changes may be classified under polymorphic radiation because as matter of fact the components in question evoluate in different directions. This is, however, somewhat formal, since it is possible to admit that e.g. concave and convex E^3 cell-portions (figs. 31, 32) derive their form from narrowly localized basipetal dislocations the only distinction being that the corresponding influence is directed between the nervures in the former case and along them in the latter. Still more evident

it is in the cuneiform modifications (figs. 33, 34) while for the bi-arcuate ones (figs. 35, 36) a supplementary hypothesis may be proposed that the influence area is splitted into two that act in every cell along some two sub-internervural lines. If so the concave and convex modifications may be considered as parallel only admitting that the factor in question, i.e. basipetal force, is directed internervural in the former case and nervural in the latter. If this interpretation does not fit exactly our definition of parallel evolution and seems not to suit to the antimere ocellar series it cannot be denied that the phenomenon in question stands in general nearer to parallelism than to polymorphosis.

Another form of the phenomenon to be named b i c o m p o n e n t a l consists of the appearance of antimerism in two neighbouring stripes thus often leading to their fusion. So e.g. convex E^3 cell-portions and concave M^1 ones fuse into E^3+M^1 in *Satyrus palaearcticus* (fig. 219, p. 39) and *Erebia pawlowskyi* (figs. 216, 217). Similarly in *Satyrus regeli* the first cell-portion of the Medial system ($M^1M^2{}_1$ in fig. 194, p. 35) breaks off from the rest and becomes an independent component. Let us consider the last example somewhat closer. The separation of $M^1M^2{}_1$ is due to the fact that the 1st cell-portions of M^1 and M^2 become convex and concave resp., come into contact accordingly and a nervural constriction followed by a division of the Medial system is resulted in. As far as the indicated cellportions being curved in contrary directions are antimere and as far as they belong to different components one might suppose that they are influenced by independent factors just as it is supposedly the case when e.g. E^3 shows concave cell-portions while those of M^1 become convex as e.g. in *Erebia ocnus* (fig. 223). But the case of the Medial system is different since the budded off $M^1M^2{}_1$ fragment is of symmetrical structure. Symmetry is one of the most fundamental properties of the Medial system at all and its existence is evidently due to the work of a factor, or a group of them, that moulds the system in its whole, and the appearance of a round-shaped symmetrical $M^1M^2{}_1$ is evidently due to this sort of influence. Hence if in the above *Erebia* the antimerism of E^3 and M^1 cell-portions can be hardly dependent upon less than two non coordinated factors with the result that the interspace between the stripes shows no inclination to symmetry, the antimerism of M^1 and M^2 in *Satyrus* is of different nature and its symmetrical character makes possible the idea that it depends upon a single factor.

Having established this one might suppose that the described difference of *Erebia ocnus* and *Satyrus regeli* depends upon the fact that the components in question belong to different systems in the former species (External and Medial) and to the same in the latter (Medial). It seems natural that every system of components has its own determinants of shape. This is, however, not always so. In *Satyrus palaearcticus* (fig. 219, p. 39) there is a series of symmetrical ring-shaped components which result from the fusion of the third Externa and first Media (E^3+M^1). All the above said concerning the origin

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of $M^1M^2$1 of *Satyrus palaearcticus* may be repeated here, viz. the cell-portions of E^3 and M^1 become convex and concave resp., come into contacts and the division of the area lying between them (E^3+M^1) and of the stripes themselves is resulted in. Evidently the process is again governed by a single factor or by a coordinated group of them. The difference, however, is that in *S. regeli* the stripes in question belong to a typically symmetrical system while in *S. palaearcticus* their original systems are different and generally show no special dependence upon one another. The only explanation available is that in the area betwen E^3 and M^1 a new factor of symmetry makes its appearance that subordinates components lying near by irrespective of their systemic appertaining. *S. palaearcticus* does not stand alone here since *Erebia pawlowskyi* (figs. 216, 217) shows exactly the same nervural fusion of E^3 and M^1. Symmetrical arrangement and structure in E^3 and M^1 have been recorded by me also in *Euptychia* (Satyridae), *Clerome* (Amathusiidae) and *Lucinia* (Nymphalidae) where it may be ascribed to the action of eye-spots (B.N.S. 1929, p. 46) and seems to generally not unfrequent. Thus bicomponental antimerisms leading to fusions seem to depend upon factors of symmetry.

We have seen that the phenomenon of antimerism besides characters of its own reveals a connection with both polymorphic radiation and parallelism. It deserves a further analysis yet and being apparently less widespread than the two indicated general principles it will be left out of consideration in the next section.

5. INTERDEPENDENCE OF PARALLELISM AND RADIATION.

Having discussed the principles of polymorphic radiation and parallel evolution we have now to consider their rôles in the origin of morphological diversity. We have seen that parallel evolution is based on the appearance of modifications, i.e., on the results of polymorphic radiation. It would be, however, totally erroneous to draw a conclusion from this dependence that parallelism is a principle of secondary importance. We have already seen that the number of modifications recorded in our nine genera is much inferior to that of the colour patterns in the group. Were every modification restricted to a single form no diversity similar to the existing one would be possible. This is, however, just the moment when parallelism enters the stage, and changes the state of the things totally. The fact is that a number of polymorphic modifications occur in more than one genus, and this very simple circumstance serves an adequate basis for the existing diversity of forms. We have seen that parallel recombinations of unmodified components may bring about but a very poor result. On the other hand polymorphosis alone cannot cover the fact as well. But if two principles work together the result is different. A single modification if reproduced in several morphological environments, be the

latter those of a form, species, genus, family and so on, may result in a great number of patterns. This is evidenced by all our parallel series. Every of them comprises individuals differing from one another rather widely but at least one character they have in common, viz., a parallel one. This is how a single modification partakes in several patterns. On the other hand a single component may undergo more than one modification, every of the latter may serve a basis for parallel series, and thus a new array of patterns arises. It should be remembered here that every component representing an integral part of the morphological environment may undergo modification in its turn and serve a basis for parallelism. But the main conclusion to be drawn from the above may be formulated as follows.

Prototypical components represent a basis from which evolution begins. The principal way of the latter is the property of every single component to be shaped into several forms, i.e., the principle of polymorphic radiation. The number of indicated modifications is, however, not great. But the results of the polymorphosis are "multiplied" as it were by repeating every of them in several morphological environments this being the essence of parallelism. Thus when the work of the two principles is combined the imaginable multitude of patterns seems rather to surpass the existing one than lag behind it.

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This is the most general idea to which the facts expounded in the present paper lead. Because, however, the phenomenon of morphological diversity is of a very complicated kind it is natural that the above comparatively simple formulation needs corrections. There are two of them both touching parallelism, one of restricting sort and another of amplifying one.

It may be regarded as established fact that some of the modifications evolved by way of polymorphic radiation occur but once. It is enough to say that only in some five modifications of the first Media out of eighteen the fact of parallel occurrence has been recorded. As to the remaining thirteen some of them as, e.g., those represented in figs. 140, 146, 149, 155, 163 are so peculiar that it seems very unlikely to meet them even beyond the limits of the Satyrid family. If so, and I think it is a general rule, the efficiency of parallelism proves to be essentially limited, and, e.g., the prediction of new forms, successfully carried through by VAVILOV, in plant parallelism, can be practised in the present case only with a very great caution. Parallelism may be regarded as one of forms of a still simpler principle of combination, dealt with elsewhere by me (1926). But it is beyond of any doubt that the number of existing combinations in the wing-pattern is much inferior than it seems theoretically possible. The absence of E^2 and presence of E^3, the absence of M^2 and presence of M^1 belong to the commonest combinations. But none of reverse combinations i.e. presence of E^2 and absence of E^3 or present M^2 and absent M^1 have been recorded. In the eye-spots we have recorded no more than five or six typical combinations (figs. 58—65) while a simple mathematical calculation

affords several hundreds of them were the 15 components of the ocellar series combined freely. Som modifications are very common, and serve a good basis for parallelism. There are others occurring but seldom, and the numerous empty quadrangles in our parallel series illustrate this very well. But finally there is the last already indicated category of modifications that occur but once. Obviously only a very restricted amount of parallel evolution may start from the rare modifications and none at all from those that occur once. Speaking otherwise the constance of both the components and their modifications is different. E^3 and M^1 are very constant components, E^2 and D^2 much less so. Similarly the oblique M^1 is a constant modification, a "perforated" M^1 (fig. 146) is unique. Because the number of rare and "once met with" modifications is considerable while that of frequent ones not very high the possibility of parallel evolution is much narrower than it might seem. Only a part of modifications is "used" the rest being beyond the action of this principle.

This circumstance lowers of course its effectiveness, but the latter is on the other hand favoured by still another phenomenon. We have seen that polymorphic radiation is a gradual process. Every stage of it is represented by a real individual. To show a transition from prototype to a modified condition a number of specimens is required sometimes belonging to different species. Now the point is that not only the final condition of the process may serve a basis for parallel evolution but the same is the case of every transitional link. Thus a given modification of polymorphosis type affords more than one starting point for combination and parallelism and consequently the efficiency of the latter principle lovered as we have seen owing to the rare occurrence of many modifications is again augmented by the just indicated circumstance.

Polymorphic radiation and parallelism may be compared to one another by means of the following diagrams. Suppose a given component may radiate from the prototype five directions *A B C D E*. If the latter occur each in one genus, or species, or form the condition resulted in may be represented in fig. 262. This is pure polymorphic radiation. If, however, every of the modifications *A—E* occur more than in one genus, species or form, the diagram represented in fig. 263 would correspond to the state of the things, when every of the final conditions is reached by several independent lines of development. Four arrows pointing to *B* and three to *C* mean that the modifications *B* and *C* arise in four resp. three genera, or species, or families, i.e., by way of parallel evolution. It has been pointed out already that polymorphic radiation and parallelism have been recorded and described by many authors. It is out of doubt that their occurence is extremely wide both in animals and plants. We have seen, however, that some facts, like e.g. antimerism cannat be classified quite smoothly under the above two principles and consequently the latter though covering a very great proportion of facts, do not embrace the whole of them. At the present period of the development of morphology, the latter in spite of

its very old age being still in a not advanced condition, these principles may be regarded as efficient tools when putting in order the facts of morphological diversity, and thus contributing something to the general problem of evolution. It is, however, a great amount of work to be done before the above principles give rise to something that would derserve a proud name of morphological laws.

SUMMARY.

In three preceding papers (1929, 1931, 1935) it is shown that a great number of wing-patterns occurring in nine palaearctic genera of Satyridae (*Satyrus, Oeneis, Melanargia, Pararge, Epinephele, Aphantopus, Erebia, Coenonympha* and *Triphysa*) originate from a prototype unifying numerous wing patterns of several Nymphaloid families of butterflies (B.N.S. 1924). In the present conclusive part of the work an attempt is made to show that almost the whole of the pattern evolution recorded in the above genera is governed by two well known principles, viz., polymorphic radiation (divergency) and parallelism. By the former principle the fact is meant that every pattern component may evoluate in several directions and thus be transformed into a number of modifications diverging widely both from the prototypical status and from one another (cf. figs. 126—163, pp. 25, 29). This is the basic principle of evolution. Without its being at work no considerable morphological diversity is possible if any.

Parallelism may be described as the occurence of one of the polymorphic modifications in several "morphological environments" meaning by the latter the total of organismal characters except for that in question, i.e. parallel one. Species, genera, families etc. may serve as the above environments if they resemble one another in some parallel characters. In the present paper only intergeneric parallelism is dealt with and 29 examples of it given (cf. parallel series I—XXIX figured in the text).

It should be emphasized that prototypical resemblances by no means may be qualified as parallel the latter concept comprising those of modified components only. A comparative method to distinguish prototypical and modified conditions is given (figs. 253—261, p. 51).

The effect of polymorphic radiation is limited by the circumstance that the modifications brought about in the individual components are not very numerous. The effect of parallelism is also limited because some modifications occur either seldom or only once not being likely to be discovered beyond the nine genera studied as well. Thus none of the two principles is sufficient to reduce under them the total of morphological diversity. But as far as many polymorphic modifications show parallel occurrence the effect of polymorphic radiation is "multiplied" by that of parallelism with the result that the two

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principles working together seem to cover a great proportion of morphological diversity.

Some phenomena of more particular character are met with in the evolution of pattern components. By intercomponental parallelism the occurrence of a given modification in several components of the same individual is meant. It may lead to homomorphic patterns. By antimerism a curvation of pattern components in two opposite directions is meant. The antimere forms thus resulted in represent mirror images of one another. If antimerism affects two neighbouring components, even belonging to different systems, their fusion into symmetrical structures may be brought about.

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PERUNIUM URSOGULO ORLOV, A NEW GIGANTIC EXTINCT MUSTELID (A CONTRIBUTION TO THE MORPHOLOGY OF THE SKULL AND BRAIN AND TO THE PHYLOGENY OF MUSTELIDAE)

BY

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INTRODUCTION.

Notwithstanding the wide paleontological range of distribution of fossil Mustelidae and studies carried on since many years past some features of their organization have remained somewhat obscure till now. Nor is the phylogeny of Mustelidae quite clear. The non too abundant, but very well preserved

material in the Paleontological Institute of the Academy of Sciences of the USSR, kindly submitted to me for the study by the Geological Museum of the Academy of Sciences of the Ukrainian SSR (Kiev) still throws some light on the aforesaid questions.

The study of the material was at first entrusted to the late Prof. V. I. Krokos, who supposed to have to do with a new genus of Guloninae. There appeared 3 references to this carnivore as to a glutton in the papers 1) by A. N. Voznesensky (1937, p. 60, Pliogulo gigas n.gen.n.sp., nomen nudum); 2) by I. G. Pidopličko (1938, p. 170, Plesiogulo) and 3) by A. N. Voznesensky (1939, Plesiogulo). The untimely death of Prof. V. I. Krokos prevented him from studying this interesting carnivore. As will be shown below the study of these remains has proved, that Perunium stands far apart from all the known subfamilies of Mustelidae and differs from them in a greater degree, than they do from each other. Consequently Perunium should be separated together with Eomellivora Zdansky into a new extinct subfamily Peruniinae, including glutton-like rather than Mellivora-like gigantic martens.

Fam. MUSTELIDAE SWAINSON 1835.
Subfam. Peruniinae subfam.nova.
Perunium ursogulo gen.n.sp.n.[1]

Pliogulo gigas nov.gen. et nov.sp. Voznesensky, A. N. 1937. Deposition Conditions of Meotic Fauna in Grebeniki Village. Aacad. of Sci. of the Ukrainian SSR. Geological Series (Geological Journal, vol. IV, fasc. 1, p. 60), Kiev. Nomen nudum.

Plesiogulo. Pidopličko, I. G. 1938. Materials for the study of fossil fauna of the Ukrainian SSR. Fasc. 1, p. 170. Academy of Sciences of the Ukrainian SSR, Inst. of Zoology and Biology, Kiev.

Plesiogulo. Voznesensky, A. N. 1939. Depositions Conditions of the Meotic Vertebrates in the Village Novaja Yemetovka, Odessa District, Ukrainian SSR, Academy of Sciences of the Ukrainian SSR. Inst. of Geology, Journal of Geology, vol. VI, fasc. 1—2, Kiev.

Locality: Grebeniki, Tiraspol District, Moldavia. Locality described by A. P. Pavlow (1915) and A. N. Voznesensky (1937). Fauna described by M. V. Pavlow (1908, 1914, 1915) and V. I. Krokos (1939). Age: Meotic. Material: Skull (No. 268) with incomplete mandibular rami (Nos. 269 a and 269 b, Geol. Inst. Acad. Sci. Ukrain. SSR., Kiev).

The figures 5, 8—10 and 12 have been drawn by Professor A. P. Bystrov, the others by Mr. N. A. Yanshinov.

[1] Perun was a god of the ancient Slavs.

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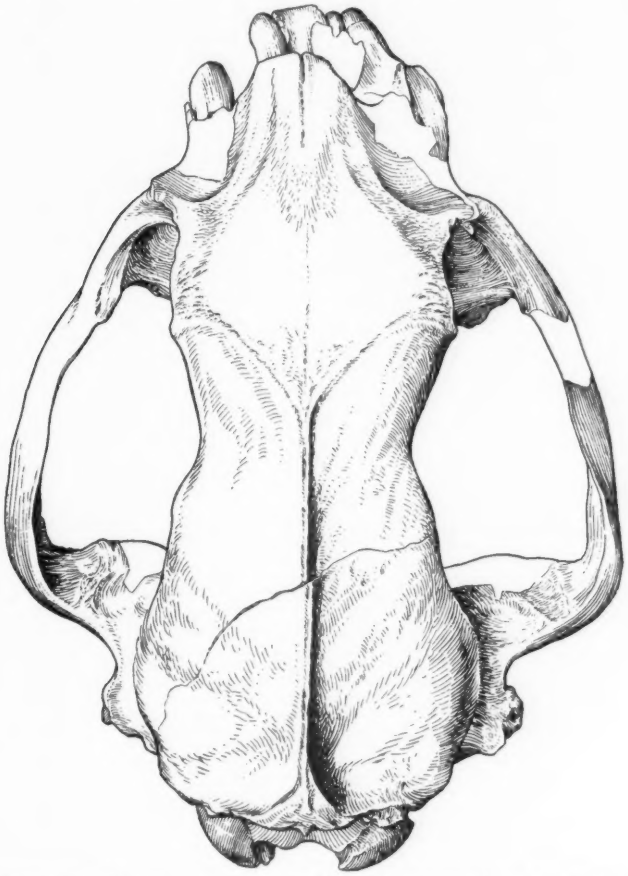

Fig. 1. *Perunium ursogulo gen. et sp.n.* Skull No. 268, dorsal view. Grebeniki. Diminished.

Skull considerable larger than in largest specimens of Gulo luscus, while the length I—M^1 is only slightly greater. It has a relatively 1) shorter snout and 2) larger and more capacious brain case.

Brain-case, like that of the polar bear, is 1) high; 2) its basicranial part, unlike—other mustelids, narrow; 3) lateral walls steep; 4) squamosal part nearly vertical; 5) mastoid small; 6) mastoid process small and but slightly diverted laterally; 7) there is a fossa on either side of sagittal crest at its junction with the transverse crest.

The brain-case of Gulo, Martes, Meles, Mellivora is 1) relatively low; 2) its base is wide; 3) parietals descend gently; 4) squamosal partes descend also gently; 5) mastoids are large; 6) mastoid process is large and reaches laterally nearly as far as does the zygomatic arch; width of the base of skull across the mastoid processes is, in nearly any adult Gulo, not less and often greater than

in Perunium; 7) there are no fossae at the junction of the sagittal and transverse crests.

Interparietals are fused to the adjacent bones.

Transverse (occipital) crest is strong and subdivided, in its upper part, into an inner and an outer crest. Sagittal crest is by far weaker than in Gulo, and there is no large hooklike process overhanging the occipital foramen. The distance of the occipital end of the sagittal crest to the brain is 18 mm.

ZEUNER (1934) calls attention to the relations between the dimensions of the occipital end of the sagittal crest and the posture of the head in recent rhinoceroses. I have found no such data of carnivores, but analogous relations are not excluded. Then we should be justified in expecting more horizontal posture of the head in Perunium, than in the glutton.

Supraoccipital bears a swelling like that in Martes, but less distinctly pronounced. This swelling is caused by the vermis of cerebellum.

Occipital condyles are placed in relation to the occipital foramen as in glutton. Paroccipital processes are not large; their apexes are absent, but they probably had the same pyramidal shape as in glutton. On the ventral side of basioccipital there is a fossa characteristic of many mustelids. In front of this fossa a small sagittal crest extends, wider and more rounded than in *Gulo*.

Bulla tympani is peculiar and apparently thick-walled. It is shorter and narrower than in *Gulo* and other mustelids, but higher medially; here it has the shape of a blunt cone from which a gently sloping crest extends laterally along the ventral wall of the external auditory duct. Of this crest, the hind slope, larger and gentler, is directed laterally and posteriorly; the anterior one, smaller, and with a concavity, runs forward, towards the base of the zygomatic arch. Medial sides of bullae are nearly vertical. The bulla resembles that of the brown bear rather than the large and thin-walled bulla of the mustelids. Tympanicum is considerably thicker than in *Gulo*, due to the presence of the mentioned crest; the inner diameter of the external auditory meatus is even absolutely smaller than in glutton. The ventral wall of the meatus, formed by the tympanicum, is shorter than in *Gulo*. The mastoid process is short, resembling that of the polar bear rather than that of the glutton.

Parietals are strongly convex laterally, due to the considerable volume of the cerebrum and of its frontoparietal prominence in particular; this results in the steep incline of the lower parts of the parietals and the nearly vertical position of the squamosals. The temporal squama is almost vertical, reaching the level of f. opticum. The thickness of the squamosals on the level of the upper edge of the occipital condyles is 10 mm.

The postglenoid process encircles the condyloid process of the mandible less completely than in the glutton. The preglenoid processes (broken away) were less strong than in the glutton. The zygomatic process of the temporal is less strong than in the glutton, rises dorsally to a lesser height and less steeply, and

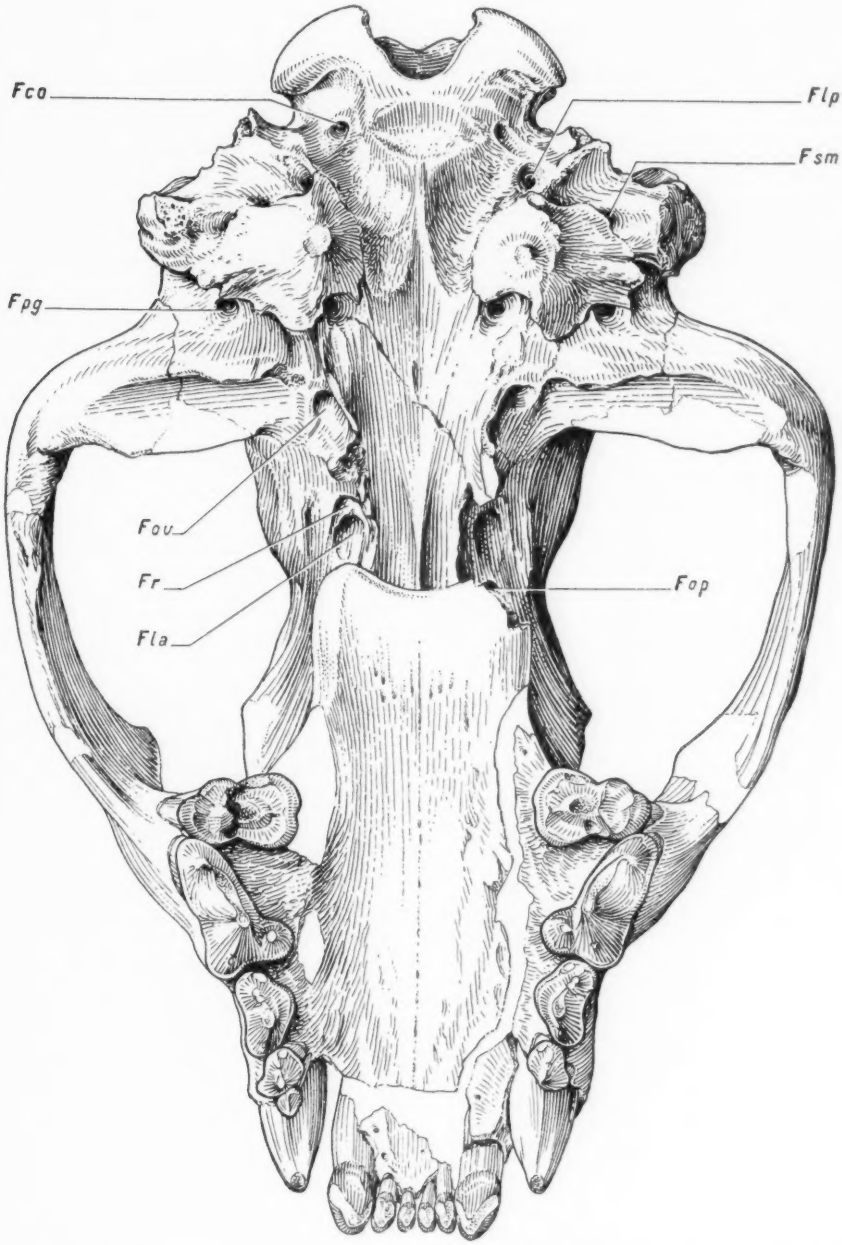

Fig. 2. *Perunium ursogulo gen. et sp.n.* Skull No. 268, ventral view. Crushing of praemaxillaria restored. Grebeniki. Diminished.

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passes into the zygomatic arch more gently. The temporal fossa due to a very slight development of the postorbital processes has a wide communication with the orbit, as in *Martes*. The zygomatic arch, seen from above, is as wide, as in *Gulo*, being however far less strong. Another distinction is the low position of the arch.

Frontal region is wide, bear-like, as in the glutton, delimited from the temporal region by crests (place of attachment of fascia temporal.). These crests, as compared to those of the glutton, are weak. The postorbital processes of the frontals are practically absent. Upon opening of the skull well-developed air cells became visible. Nasals are short, their distal ends highly raised dorsally; their longitudinal axes are nearly parallel to the base of the skull, the height of the snout being greater than in the glutton. The nasals are thickened ventrally along the suture to form a crest.

Maxillaries bear a large fossa for the m. levator labii superioris which points to a considerable mobility of the upper lip and the tip of the snout. Infraorbital foramen is large as in marten: its external wall is thin; the opening is rounded oval, with the long axis slightly inclined medially. The trochlear spine for the m. obliquus superior is well preserved. Its size in the glutton is very variable. The alveolar edge of the maxilla is thin, the alveoles being very pronounced externally, especially sharply so the antero-external root of P^4 corresponding to the paracone, which reaches f. infraorbitale. The palate is gently arched with no traces of a low sagittal crest typical of the glutton.

On the lacrimal, the lacrimal sulcus is much wider and deeper than in the mustelids. The lacrimal duct, filled with matrix, seems to be also better developed than in other mustelids. The orbit is of a considerable size. From the postorbital process of the frontal a crest runs downward and backward, ending at the level of the f. rotundum (V_2), bounding from the dorsal side of the skull the orbit and the region of the foramina for the II—VI nerves. This latter area is bounded ventrally by a crest, running from the lacrimal duct toward the base of the alisphenoid where it ends medially from the f. rotundum. These crests as well as the shape of the skull region between them, are quite similar to those in adult skulls of bears.

Skull openings. Anterior condyloid foramen (fig. 2, *Fco*), for the XII nerve, lies on a level with the posterior edge of the paroccipital process (in the glutton, on a level with the anterior edge of the latter). It opens together with the opening for vessels.

On the inner side of the exoccipital there is, as in a number of Arctoidea, an osseous bar closing vessels. Two canals open into the f. lacerum posterius (= f. jugulare externum): the c. nervi hypoglossi, and the canal for the a. meningea posterior.

Foramen lacerum posterius (= f. jugulare) (fig. 2, *Flp*) for IX, X and XI cranial nerves and v. jugularis interna is round, and larger and placed much

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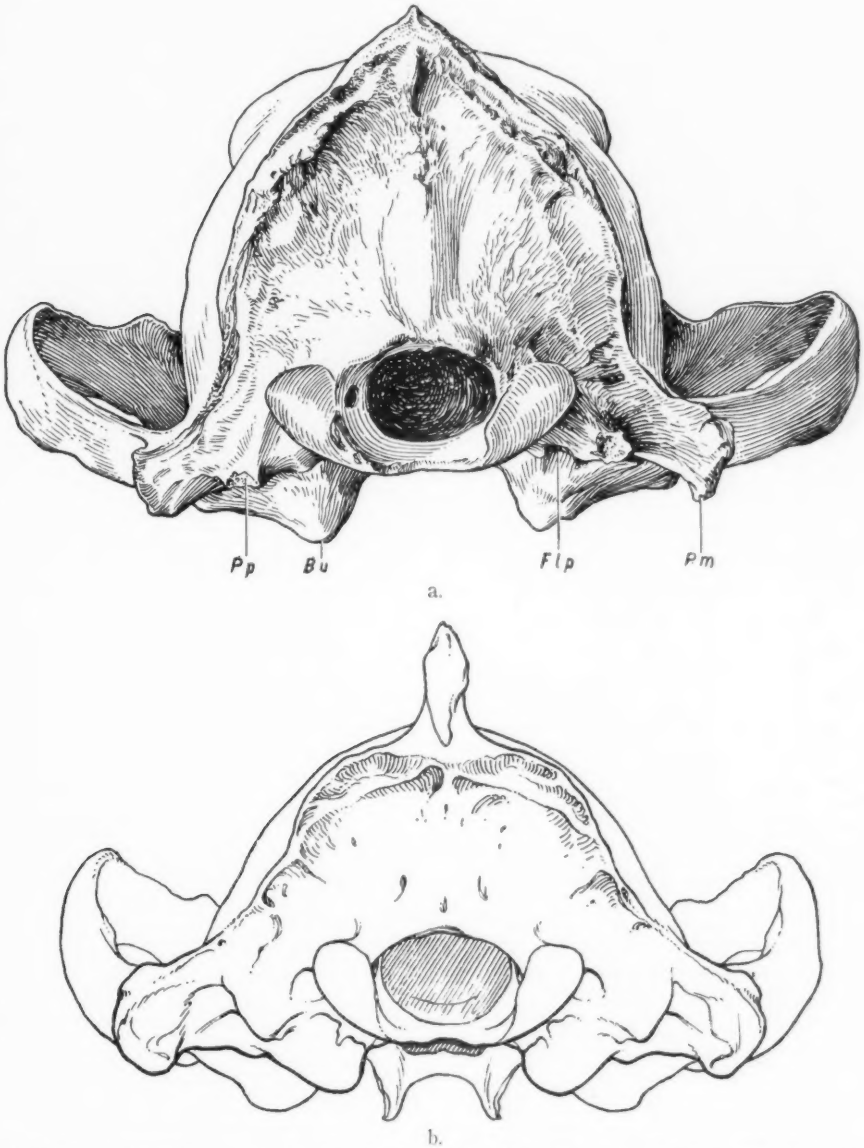

a.

b.

Fig. 3. a.—*Perunium ursogulo gen. et sp.n.* Skull No. 268, occipital view. NB. the protuberance above the upper border of the foramen occipitale magnum corresponding to the vermis of the cerebellum. Grebeniki. Diminished. b.—*Gulo luscus L.* Skull No. S 1613, Zool. Mus. of the State University of Moscow, occipital view. Diminished.

more anteriorly from the foramen for the n. hypoglossus than in glutton, possibly due to the greater length of the basicranial part of the skull. The right caroticus canal is separated from f. jugulare and lies in front of it; on the left

side the two openings are fused. The stylomastoid foramen (fig. 2, *Fsm*) of the VII nerve is placed within a considerable distance from f. jugulare. Unlike in *Gulo* and *Martes*, the two openings are not divided by the posterior part of bulla, the latter lying in front and medially of the straight line connecting the two, as in the polar bear. The median lacerate foramen (f. lacerum anterius of German authors), like in the bear, is very large and divided by an osseous lamina into a ventral and a dorsal part.

The foramen of the osseus Eustachian tube is large, oval in shape. The postglenoid foramen (fig. 2, *Fpg*) is large and rounded. The external auditory meatus is quite small.

The oval foramen (fig. 2, *Fov*) (V_3), of an oval shape, as in the martens, is large, corresponding to the large size of the lower jaw. It is covered, medially and ventrally by a laterally inclined posterior lamellar part of the alisphenoid, as in the marten. Alisphenoid canal is absent. Foramen rotundum (fig. 2, *Fr*) (V_2) is small. F. lacerum anterius (= sphenorbitale = sphenoideum) for the III, IV, V and VI nerves (fig. 2, *Fla*) is directed, as in the bear, more upward than in the glutton. Foramen opticum (fig. 2, *Fop*) is small.

The four last openings (for the II, III, IV, V, and VI nerves), as in the bear, lie almost along the same straight line, and are all of them visible when viewed from the front through the orbit on a level where the frontals are narrowest.

Upper dentition (figs. 2, 4, 5). The general appearance is typical of the mustelids. The length of the row I—M^1 is only slightly greater than in large recent gluttons, the dentition being relatively weaker than in *Gulo*. The tooth enamel is smooth.

I^1 is strongly laterally compressed. On the posterior side of the incisors a well-developed cingulum forms a heel. I^2 has the same structure, being markedly larger. I^3 is still much larger, somewhat canine-like. Laterally, there is a groove, running from the apex to the base, caused by abrasion of the tooth by the lower C; medially, a small groove produced by the external I_3.

C follows after a short diastem (6 mm); it is rather slender and slightly curved backward, with a vestigial posterior vertical crest.

P^1 is preserved on the left side, placed almost without a diastem behind the canine and pressed closely to P^2. The transverse diameter is greater than the antero-posterior one. On the posterior longer side, a vestigial secondary cusp is present. On the inner side of P^1—M^1 there is a well-developed basal cingulum.

P^2 is considerably larger, the base of the crown is subtriangular. Along the crown a crest, bearing posteriorly a small, secondary cusp. P^3, on the left side, follows closely the preceding one. It is similar to but much larger than P^2. The longitudinal crest bears three small secondary cusps, one on the parastile, the two others, posteriorly. These latter are fused with their bases, as a result of which the worn cusp enamel forms an "8". The posterior basal cingulum

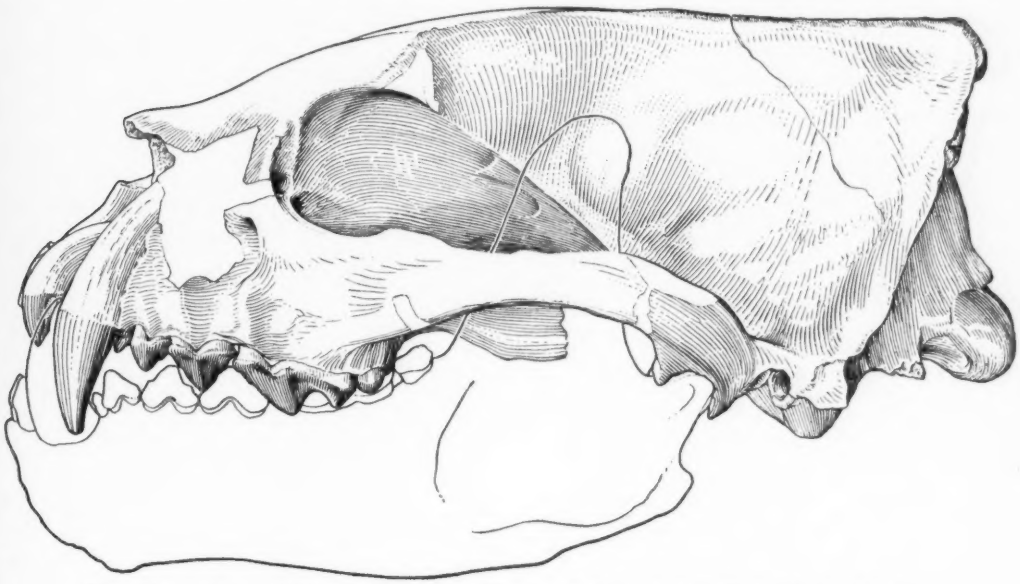

Fig. 4. *Perunium ursogulo gen. et sp.n.* Skull No. 268. Lateral view. Owing to the deformation the snout is raised and seems to be shorter then the lower jaw. Grebeniki.

carries a pit formed by the wearing action of the top of P_4. Externally, the crown base, like that of P^2, is slightly concave. Of the three roots, one posterior is lingual. P^4 is very much like the corresponding tooth of the marten. The inner cusp (protocone, resp. deuterocone) is an obtuse low cone, not separated by a constriction from the paracone. On the parastyle, there is a distinct small secondary cusp. The robust anterior lateral root of P^4 reaches the level of the lower edge of the infraorbital foramen.

M^1 is very large, its crown-base being but slightly smaller than that of P^4; in general proportions it closely resembles M^1 of the marten.

The lingual surface of the walls of alveoles is rough due to the firm attachment of the gums. The posterior wall of the alveoles of both the M_1 has split off, but it seems to have been thin; in any case, no incipient M^2 may have been present here; this is confirmed also by the nature of grinding of the crown of M_2.

Mandible (figs. 5 c, d, 6, 7). Noteworthy is the great height of the jaw, the strong development of the symphisial part, and a somewhat "hyaenoid" appearance. The lower edge is not convex, but straight, and even slightly concave. The inner side of the alveolar edge, from the symphysis up to the anterior end of M_1, is rough, as is the case (in a very different degree) in the glutton. The condyle is semicylindrical, thicker in the medial part and thinner laterally. The angular process is short, thick, slightly bent medially. On the inner side, the tuberosity of the m. pterygoideus internus is well developed.

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Table 1.

Skull No. 268 Perunium ursogulo g.n.sp.n.	Gulo luscus S. No. 1613	
Length from anterior border of I^1 to back of occipital condyles .	191.5	159
Length from anterior border of I^1 to lower border of foramen magnum	180.5	111
Length from anterior border of I^1 to back of palate	100.5	86.5
Length from anterior end of nasalia to back of sagittal crest	170.5	115
Length from anterior border of I^1 to fore border of orbita	66.5	61.4
Length from anterior orbita border to back of occipital condyles	146.0	84
Width of skull at zygomatic arches	134.0	107
Width of skull at postorbital processes	61.5	52.5
Width of skull (minimum) back of postorbital processes	45.0	35.5
Width of skull at mastoid processes	91.0	93.5
Bulla tympani: anterior posterior diameter	23.5	22.2
transverse diameter (bulla + meatus auditorius externus)	25.0	—
height (?)	13.0(?)	10.5
Height of occiput from the base of sagittal crest to ventral surface of basioccipitale	60.5	43.7
A—length from anterior incisor border to back of M^1—M^1	72.0	65
B—length from back of M^1—M^1 to back occipital		
Ratio—$\frac{B}{A}$	1.65	1.43
Width (external) condylus dexter-condylus sinister	48.5	39.0

Table 2.

Upper dentition		Perunium ursogulo g.n.sp.n.	Eomellivora wimani Zd.		Eomellivora ?sp.	Eomellivora rumana
		Grebeniki No. 268	O. Zdansky 1924 China		G. E. Pilgrim 1932 India	I. Simionescu 1938 Bessarabia Cimislia
			1	2		
I^1	Anterior posterior diameter	4.4	4.3	4.9	—	—
	Transverse diameter	2.4	2.6	2.6	—	—
I^2	Anterior posterior diam.	?6.0	5.4	5.8	—	—
	Transverse diam.	3.2	3.2	3.1	—	—
I^3	Anterior posterior diam.	9.0	8.5	9.3	—	—
	Transverse diam.	7.3	6.1	6.5	—	—
	Height of the crown	23 (?25)				24.5
C	Anterior posterior diam.	12.0	12.0	12.3	—	?18
	Transverse diam.	9.6	10.2	10.6	—	11
P^1	Anterior posterior diam.	3.6	3.0	3.4	—	—
	Transverse diam.	4.3	5.1	5.2	—	—
P^2	Anterior posterior diam.	8.5	6.0	6.2	—	—
	Transverse diam.	6.6	7.6	8.0	—	—
P^3	Anterior posterior diam.	13.8	14.2	14.3	16.4	—
	Transverse diam.	9.5	10.1	10.6	8.8	—
P^4	Anterior posterior diam.	22.2	21.6	21.6	—	22.0
	Transverse diam.	14.5	15.1	16.7	—	15.5
M^1	Anterior posterior diam.	12.2	11.6	12.3	—	—
	Transverse diam.	20.0	20.1	20.5	—	—
C—M^1	Length of row C—M^1	63.0	—	—	—	—

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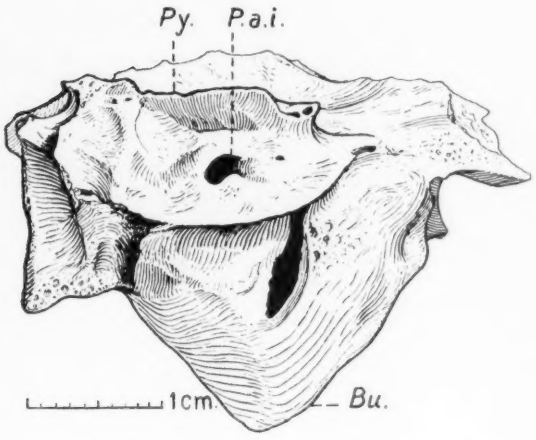
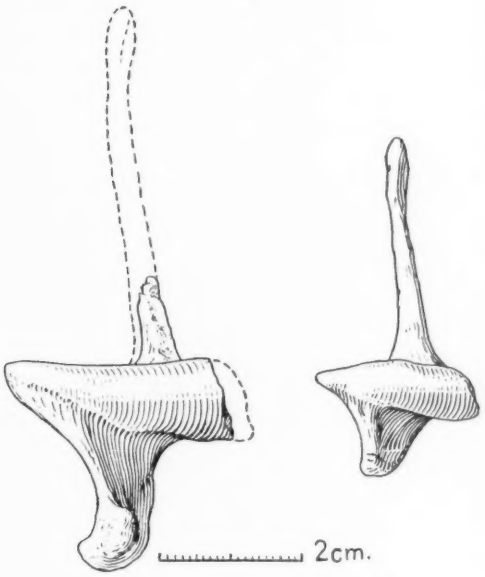


a.

b.



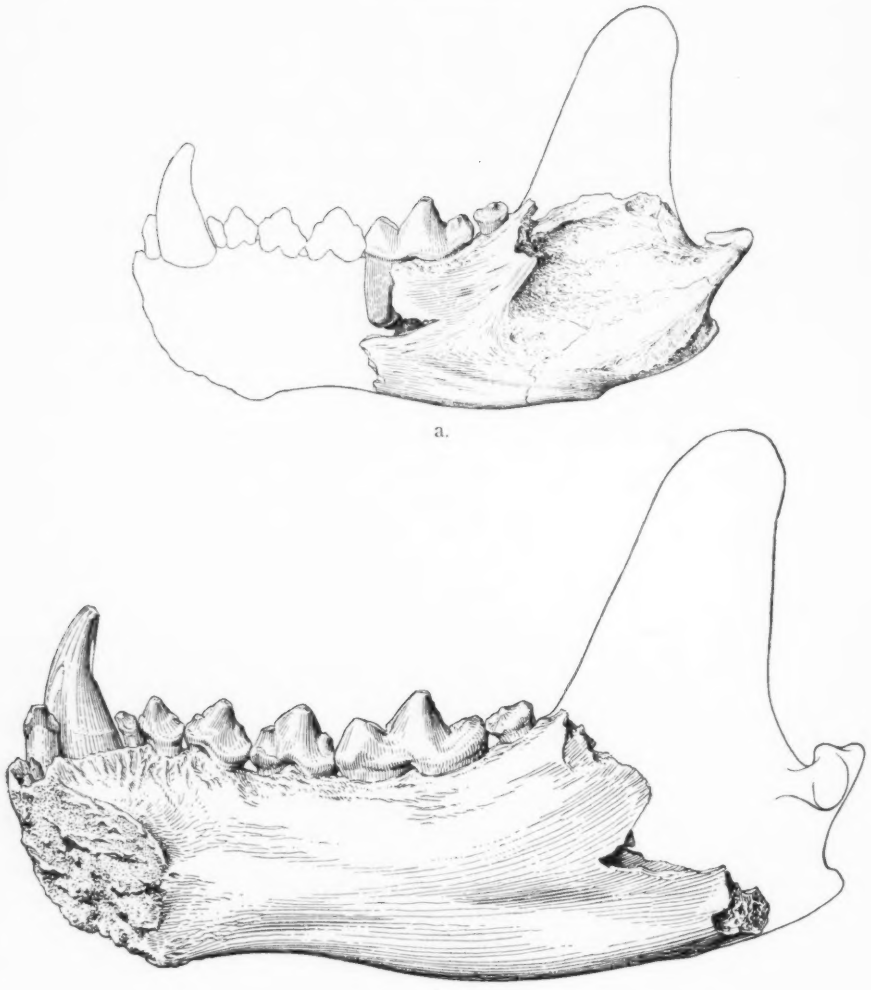
c. d.

Fig. 5. a.—c—*Perunium ursogulo gen. et sp.n.* a.—a part of the left auditory capsule of the skull No. 268, inner and posterior view. Grebeniki. × 2. b.—upper teeth of the right side, crown view. × 1. c—left mandible (Fragment) No. 269 b. hind view. Grebeniki. × 1. D—*Gulo luscus.* No. S 1613 (Zool. Mus. of the Moscow State University). Left mandible, hind view. × 1.

The lower teeth (figs. 6, 7 a) resemble at first sight those of the glutton more closely than the upper ones. Unlike in *Gulo* the tooth enamel is smooth.

L_1 is absent; judging from the root it was small and compressed. I_2 is absent; it was considerably larger and posterior in position, as in many mustelids. I_3 is still much larger.

C is high, curved backwards. The enamel is worn by the lateral wall of I^3 anteriorly and much more so medially; posteriorly, it is worn by the upper canine.



a.

b.

Fig. 6. *Perunium ursogulo gen. et sp.n.* a.—fragmentary left mandibular ramus with M_1, M_2. No. 269 b, outer view. × 1. b.—right mandibular ramus No. 269 a, inner view. × 1. Grebeniki.

P_1 is small and has a longitudinal crest and a cingulum on the inner side. P_2: the base of the crown is subtriangular. The tooth is turned with its anterior narrow edge and root outwards, and with its posterior wide root, inwards. At the base of the anterior edge of the sagittal crest, there is a small talonid; on the posterior side a secondary cusp is present. The inner cingulum is well developed. P_3 is much larger. The transverse diameter is greater than in P_4. The cingulum encircles the inner side and posterior end. There are well developed anterior and posterior accessory cusps. P_4 has a more longitudinal posi-

tion. The anterior and posterior secondary cusps are well developed. Unlike P_1 and P_2, and P_3 in particular, the posterior end is but slightly wider than the anterior. The inner basal cingulum is well developed.

M_1 is long, narrower than in the glutton. The protoconid is much higher than the paraconid, but is equally long. There is no metaconid. The hypoconid is an obtuse longitudinal crest; due to its position on the rise to the coronoid process its upper surface is on the level with the paraconid. The enamel of the external side of the proto- and paraconid is worn by the para- and metacone of P^4. The crown surface of the hypoconid is worn more strongly than the anterior surface of the protoconid, but in neither of them is this effect of the toothantagonist, but that of food.

M_2 has an oval crown with a low conical cusp in its center and a low longitudinal crest. The tooth is placed on the rise to the coronoid process, the crown being inclined forward; the crown base therefore lies higher than in M_1, the sagittal crest and the crown surface forming a continuation of the crest on the heel (hypoconid) of M_1. The anterior edge of the crown is slightly worn by the posterior edge of M^1; the posterior edge which had no antagonist is unworn.

For measurements see below.

Table 3.

Lower dentition		Perunium ursogulo g.n.sp.n.	Eomellivora aff. wimani	Eomellivora wimani	Eomellivora ? tenebrarum		Eomellivora necrophila	
					Pilgrim 1932 India			
		Grebeniki No. 269a	N. Emetovka Distr. of Odessa No. 46	Zdansky 1924	G. S. I. D. 20	G. S. I. D 243	G. S. I. D 254	
I_1	Anterior posterior diam.	—	—	2.4	—	—	—	—
	Transverse diam. . . .	—	—	1.5	—	—	—	—
I_2	Anterior posterior diam.	—	—	4.1	—	—	—	—
	Transverse diam. . . .	—	—	3.5	—	—	—	—
I_3	Anterior posterior diam.	6.0	—	6.0	—	—	—	—
	Transverse diam. . . .	4.5	—	3.8	—	—	—	—
C	Anterior posterior diam.	12.6	14.4	12.7	—	—	13.1	—
	Transverse diam. . . .	10.0	10.5	9.8	—	—	—	—
P_1	Anterior posterior diam.	4.0	—	3.5	—	—	4.2	—
	Transverse diam. . . .	4.5	—	5.1	—	—	—	—
P_2	Anterior posterior diam.	8.6	8.5	6.4	—	—	6.4	—
	Transverse diam. . . .	6.3	6.0	7.9	—	—	—	—
P_3	Anterior posterior diam.	11.8	11.6	11.8	—	—	8.2	—
	Transverse diam. . . .	9.8	8.0	8.3	—	—	—	—
P_4	Anterior posterior diam.	15.2	17.5	15.4	—	—	12.1	13.1
	Transverse diam. . . .	9.0	9.3	8.8	—	—	—	7.0
M_1	Anterior posterior diam.	23.8	26.3	24.5	22.6	20.4	21.9	—
	Transverse diam. . . .	10.0	10.2	9.1	7.1	7.4	7.4	—
M_2	Anterior posterior diam.	8.2	—	7.8	5.7	—	—	—
	Transverse diam. . . .	7.5	—	6.4	—	—	—	—
	Length of row P_2—M_1		60.7	59.0				

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Table 4.

	Perunium ursogulo n.g.n.sp.	Mellivorinae
1. Brain-case	High, narrow	Low, wide
2. Basicranial part of the skull .	Narrow	Wide
3. Bulla tympani	Of insignificant size in projection, short, thick-walled	Large, long, thinwalled
4. Meatus (osseous) auditorius externus	Short, narrow directed slightly forwards	Comparatively, long, wide, directed strongly forwards

Table 5.

	Eomellivora wimani Zdansky (O. Zdansky 1924)	Perunium ursogulo n.g.n.sp. No. 268 Grebeniki
P^2	No secondary cusps	With posterior secondary cusp
P^3	With an anterior and a posterior secondary cusps	With an anterior and two posterior secondary cusps
P^4	No secondary cusps on paracon	Paracon with an anterior secondary cusp on the parastyle
P_2	No secondary cusps	A rudimentary anterior and a well developed posterior secondary cusp
P_3	A posterior secondary cusp	An anterior and a posterior secondary cusp

In comparing *Perunium* with the other mustelids its resemblance to *Eomellivora* Zdansky (1924) is striking. Pilgrim (1932) described from India *Eomellivora* (?) *neorophila* and *E.* (?) *tenebraum*. The holotype of the latter species is the posterior part of a mandibular ramus with M_1 described under the name of *Mellivorodon palæindicus* by Lydekker (1884). Zdansky, having at his disposal only an incomplete facial part of the skull and lower jaws, referred the genus erroneously to Mellivorinae and gave it a misleading name. Pilgrim, who had a still more fragmentary material, could not correct the mistake of Zdansky, but noted that *E. tenebrarum* was probably more closely related to *Gulo* than to *Mellivora*. In comparing the skull of *Perunium* with skulls of Mellivorinae a number of differences become evident.

These differences are sufficient to show the impossibility of referring *Perunium*, as well as Eomellivora, to Mellivorinae or to another subfamily of Mustelidae. *Perunium* is farther distant from any of these subfamilies than they are from each other and consequently it should be separated, together with *Eomellivora*, into a new extinct subfamily Peruniinae, including glutton-like rather than mellivora-like gigantic martens, exceeding in size, with the exception of *Megalictis ferox* Matthew (1907), all the mustelids so far known.

Of the living mustelids, the greatest resemblance to *Perunium* is shown by the glutton. However, *Perunium* is sharply different from Guloninae not only

in the specialization of teeth, but also in the relatively less stout facial part of the skull, the weaker dentition, and the much longer and higher brain-case with slightly developed sagittal and transverse crests, the brain-case resembling most closely in the posterior half that of the polar bear but by no means that of the mustelids. The bulla tympani of *Perunium* is quite peculiar—it is small and thick-walled. The structure and strong development of the crest running from the postorbital process towards f. rotundum (the "Orbito-Temporales Trajectorium" of STARK 1935) as well as the position and direction of the exits of the II, III, IV, V and VI nerves are again very much like those in bears.

The resemblance of the posterior part in the brain-cases of *Perunium* and the polar bear is so great that it suggests an inheritance from a common ancestor of the two families of Arctoidea. But the position of the occipital condyles, the structure of the internal side of the exoccipitals the course of the condyloid canal for the XII nerve, the arrangement and proportions of the osseous bridge for the brain vessels), and the structure of the basicranial part from the ventral side, not to speak of the facial part and teeth, are characteristic of the familiy of martens.

From the table 5 (p 76) it will be seen that *Perunium* has more highly specialized teeth than *Eomellivora*.

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EOMELLIVORA aff. WIMANI ZDANSKY (figs. 7 b, c).

Locality: Novaya Emetovka on the Khadzhibeev Liman near Odessa (No. 46, Geol. Inst. Acad. Sci. Ukrain. SSR., Kiev, excav. 1935). Incomplete right and left mandibular rami.

The jaw is stout, high, symphysis massive, lower edge typically of Peruniinae straight, even slightly concave. The considerable height and stoutness impart to the jaw a still more "hyaenoid" appearance than in *Perunium*. The inner side of the alveolar edge is very rough from the symphysis up to the posterior end of M_1. Foramina mentalia on the two rami are similarly placed on a level with P_2 and P_3.

C is stout, somewhat laterally compressed. The well preserved alveole of the right canine reached with its apex the level of the posterior half of P_2.

On the right side the alveole with the root of P_1 squeezed between C and P_2 is preserved. The transverse diameter of the root is larger than the antero-posterior one; the tooth is as strongly reduced as in the Chinese specimens. The shape of P_2 is as in Chinese specimens. The anterior talonid is absent. On the posterior side of the sagittal crest, on the right P_2 there is a hardly perceptible incipient secondary cusp. The shape of P_3 is as in Chinese specimens; the tooth is much larger than the preceding one, but very similar to it, and like P_2 is turned with its anterior end laterally. On the posterior side of the sagittal crest there is a small but well marked secondary cusp. P_4 as in Chinese specimens

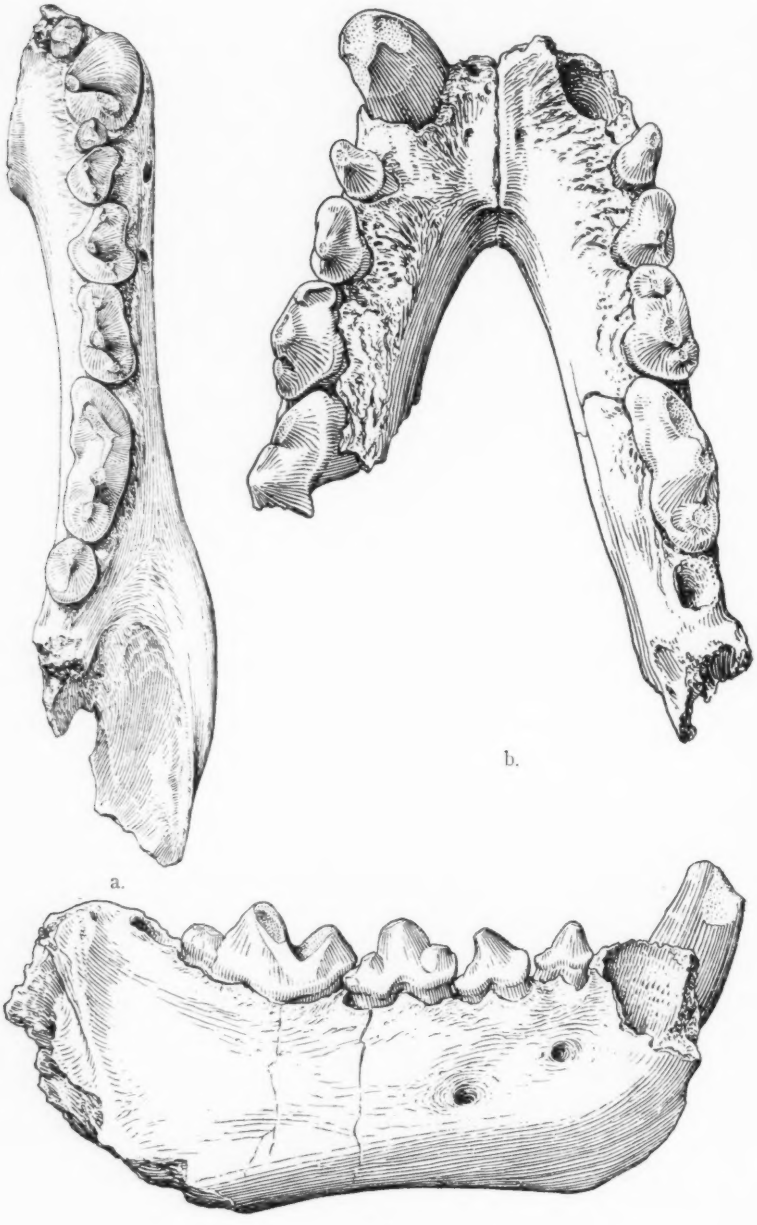

Fig. 7. *Perunium ursogulo gen. et sp.n.* a.—right mandibular ramus No. 269 a, upper view. Grebeniki. × 1. b.—*Eomellivora aff. wimanni* ZDANSKY, fragmentary mandible. No. 46, upper view. Grebeniki. × 1. c.—same mandible No. 46, lateral view. Novaja Emetovka, Odessa District. × 1.

is much longer than P_3, and is set with its longitudinal axis along the jaw. The anterior and posterior secondary cusps are well developed.

M_1 is very long. The protoconid and paraconid are worn on the lateral side. Like in the Chinese specimens and in *Perunium* the talonid consists only of the hypoconid.

This specimen is much like the lower jaw of *E. wimani* ZDANSKY (1924). The differences are: the larger size and the greater stoutness of the jaw, the somewhat larger size of the teeth, and the weaker development of the posterior (single) secondary cusp on P_3. It is possible that we have a local race of this species.

EOMELLIVORA RUMANA (SIMIONESCU) 1938. *Pannonictis rumana* SIMIONESCU.

In 1938, SIMIONESCU described from Simislia (east of Taraclia, age—meotis) a fragment of the left upper jaw with C, P^4 and alveoles of P^1, P^2, P^3, and, comparing this specimen with *Pannonictis pliocaenica* KORMOS (1931), a large marten from the Upper Pliocene of Hungary, erected for it a new species, *P. rumana*. To the latter he tentatively referred also the lower jaw previously described by him (1930) as *Lutra rumana*. A comparison of the figures by SIMIONESCU, with the skull and teeth of *Perunium* leaves no doubt that *P. rumana* belongs to Peruniinae. The absence in *P. rumana* as described by SIMIONESCU, of a secondary cusp on the anterior side of the paracone in P^4 makes it difficult to place that species in the same genus with *Perunium* and induces us to refer it to *Eomellivora*. The upper jaw from Cimişlia (resp. its dentition) is not essentially different from *E. wimani*. Nevertheless until more complete data are obtained it is convenient to retain for it the specific name *rumana*.

It is of interest to consider here the relationship between *Pannonictis* and Peruniinae.

The absence of accessory cusps in P^2, P^3, and all the lower premolars in *Pannonictis*; the presence of a well developed large metaconid and a wide "cup-like" concave talonid on M_1; a distinct wrinkling of the canines, and a number of other features, completely exclude the grouping together of *Pannonictis, Perunium,* and *Eomellivora* into one genus. This is fully supported by a comparison of the brain of *Pannonictis* described by T. EDINGER (1931), that of *Perunium*.

After the study of the material from Grebeniki and Novaya Emetovka the assignement of the lower jaw described by SIMIONESCU (1930) as *Lutra rumana* to *Pannonictis,* cannot be agreed with. Neither the size of P_3 not the profile of the lower edge of the mandible—quite otter-like indeed,—neither the position of premolars (SIMIONESCU 1930, fig. 10), do not support this

Table 6.

Genera	Species	Locality	Age, horizon
Perunium gen.nov.	P. ursogulo sp.nov.	Village Grebeniki (Grebenki) near Tiraspol, Moldavian SSR.	Meotic
Eomellivora	E. wimani ZDANSKY 1924	Eastern, China. Collection of Paleontol. Inst. Upsala	Mio-Pliocene (?Pontian). Hipparionfauna
	E. aff. wimani Zd.	Vill. Nov. Emetovka on the Khadjibeev-Liman near Odessa	Meotic
	E. necrophila PILGRIM 1932	India, Vicinity of vill. Bilhomar west of Chinji, Salt-Range. Collection Geol. Surv. India in Calcutta, No. 243	Chinji stage (Lower Siwaliks) Upper Sarmatian
	E. (?) tenebrarum PILGRIM 1932 (= Melivorodon palaeindicus Lydekker)	India, Niki, Salt-Range. Collection Geol. Surv. India, Calcutta, No. 22	Dhoh Pathan (Mid. Siwaliks) (?Lower) Pliocene?
	E. rumana SIMIONESCU nov. nomen (= Pannonictis rumana, SIMIONESCU 1938; nec Lutra rumana SIMIONESCU 1930	Cimişlia, Bessarabia, near Taraclia	Meotic

assumption by SIMIONESCU. The premolars of Peruniinae are set obliquely to the longitudinal axis of the mandibular ramus, while in *L. rumana*, along one straight line. The geological age of *L. rumana* (Meotic) and *P. pliocaenica* (Upper Pliocene) likewise does not favour the uniting of *L. rumana* with *P. pliocaenica*.

The fragmentary state of the material on *E. tenebrarum* and *E.* (?) *necrophila* and the absence of data on the variability of *Eomellivora* hamper the precise evaluation of the specific value of these findings. *E.* (?) *necrophila* is somewhat smaller than *E. wimani* and has a less steep symphysis.

DIAGNOSIS OF THE SUBFAMILY.

The new subfamily Peruniinae comprises following genera and species (see p. 2).

Mustelids of large to very large size with high short face and bear-like frontals. Brain-case high and narrow as in polar bear, with a narrow basi-cranial part and steep lateral walls. Mastoids small, mastoid process small, extending but little laterally. Bulla tympani short, subconical. Zygomatic arches broad and low in position, orbits communicating broadly with temporal fossae. Teeth closely spaced, enamel smooth except for cingulum in M^1. C with an incipient crest posteriorly, or devoid of it; P^1 single-rooted, small but functional; P^2—P^4 with basal cingula. P^2 triangular, without accessory cusps (*Eomellivora*) or

with a posterior one (*Perunium*); P^3 triangular, with one anterior and one (*Eomellivora*) or two (*Perunium*) posterior accessory cusps. P^4 stout with (*Perunium*) or without (*Eomellivora*) an accessory cusp between the anterior and lateral sides of the paracone; protocone (deuterocone) not distinctly separated from the paracone. M^1 with three cusps, of which metacone is weak; cingula well developed. Mandible deep, with a strong symphysis. P_{1-3} triangular. P_2 without accessory cusps (*Eomellivora*) or with a posterior one (*Perunium*); P_3 with a posterior accessory cusp (*Eomellivora*) or two, anterior and posterior ones (*Perunium*); P_4 with two, posterior and anterior cusps. M_1 elongate, laterally compressed, with talonid bearing a single low cusp with a sagittal crest (hypoconid). M_2 single-rooted, oval, provided with a flat longitudinal crest with a cusp in the middle.

The geological age of the European findings of Peruniinae is Meotic. *E. wimani* is not precisely dated, presumably it is Pontian. Although the correlation of the Cenozoic of India and Europe is not quite stable (PILGRIM 1913, MATTHEW 1929, COLBERT 1935, BORISSIAK 1943), it is still evident that the time of existence of Peruniinae should be regarded as Upper Sarmatian-Pontian.

The direct ancestors of Peruniinae are not known. ZDANSKY's hypothesis as to the origin of *Eomellivora* from *Bunaelurus* (Oligocene, U. S. A.) should be abandoned; judging from the structure of its teeth *Bunaelurus* could have been an ancestor of *Eomellivora*, but its large ellipsoid bulla tympani shaped as in the majority of mustelids is so different from that of Peruniinae that it quite excludes the possibility of their direct kinship. The available data enable us only to state the absense of direct ancestors of Peruniinae among the Mustelidae known to us; we can assume a comparatively early, most probably not later than the Upper Oligocene, branching off of the ancestors of Peruniinae from the common stem of martens. An indirect evidence in favour of such an early separation of Peruniinae from the ancestral stalk is the fact that already in the Oligocene a possibly direct ancestor of Putoriinae is found in the shape of *Bunaelurus*, and in the Miocene, badgers, highly specialized otters (*Potamotherium*), etc. are already present. The birth-place of Peruniinae should probably be sought for in Central Asia, and possibly also in North America.

THE BRAIN OF PERUNIUM (figs. 8—10).

Unfortunately during the preliminary preparation of the skull prior to its being sent to me, the rock filling the foramen occipitale magnum and a considerable part of the cast of the cerebellum was removed. Distinct casts of arteries on the lateral surfaces of the brain cast, the frontoparietal prominence and sinus venosus sagittalis superior are preserved proving that we are dealing

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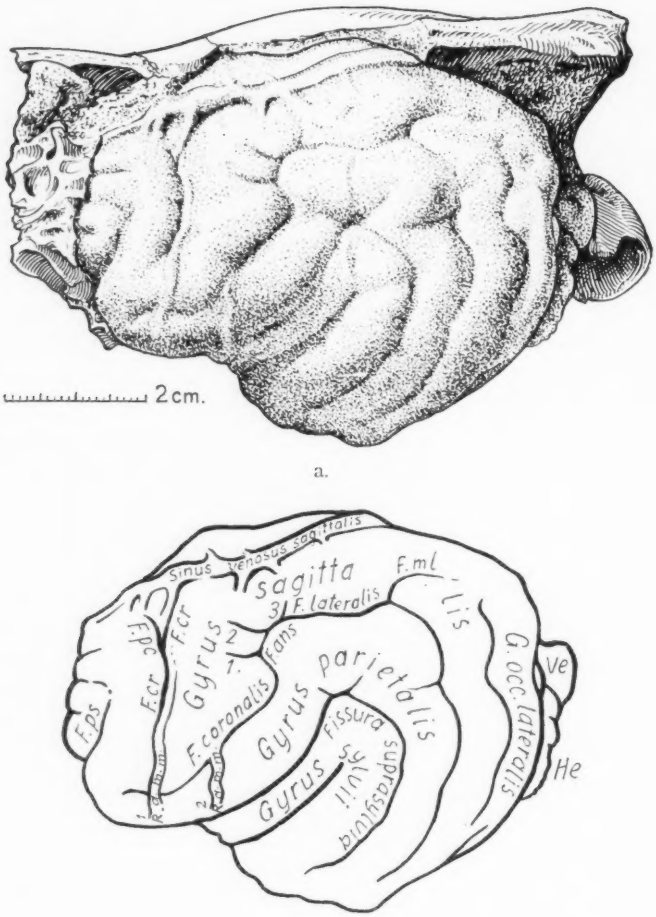

Fig. 8. *Perunium ursogulo gen. et sp.n.* a.—the natural endocranial cast of Perunium ursogulo gen. et sp.n. of the skull No. 268, dorsolateral view. Grebeniki. × 1. b.—scheme to the figure a.

with a cast of the brain together with the brain membranes, the dura mater included.

Cerebrum (Left hemisphere). In small carnivores, martens in particular, the internal side of the brain-case shows all the most characteristic fissures and convolutions.

Mustelids have never been laboratory animals; hence, in their brain neither the localization, nor even the internal structure of the gray matter have been studied. Thus all the assumptions concerning the functional significance of some or other areas of the cortex of *Perunium* may be based only upon the data obtained for dogs.

Table 7.

Cerebrum dimensions	
1. Sagittal length of the telencephalon	?83 mm
2. Anterior border of prominentia frontoparietalis—posterior occipital border of telencephalon	69 „
3. Height on the level of prominentia frontoparietalis	32.6 „
4. Height of the level of the parietal prominentia of gyrus sagittalis	51 „

A second essential point is the variability in the shape, size and interrelations of the fissures and convolutions within not only of the same species but even of the same individual (right and left hemispheres). This variability is recorded usually in small secondary fissures and convolutions, much rarer in larger, main ones, especially in the brain of Carnivores, relatively poor in fissures and convolutions. The main fissures and convolutions are fairly persistent; moreover, they only are reflected on the cast.

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In the brain of Carnivores KRUEG (1880) distinguished: 1) boundary fissures, 2) main fissures and 3) secondary fissures. The first of these, appearing in ontogeny earlier than the others, delimit the base of the hemispheres resp. its olfactory centres and tracts from the remaining cerebrum; the main fissures divide more or less the hemispheres into main lobes and convolutions. Latest to appear and most variable in number, size and shape are the secondary fissures. The fissures are described further in this order.

When viewed from above the cerebrum may be compared to a high isosceles trapezium, crowned with a low isosceles triangle with its apex directed forward. When viewed from the side it is on the whole of the same shape as in the glutton. A closer examination reveals the following peculiarities.

The frontal lobe, lying in front of the cruciform fissure, is distinguished from that in other large mustelids (the glutton, the badger especially) by a relatively small size.

The parietal lobe strikes one by the strong development in the dorsal direction of the sagittal (3rd) convolution on the level of the upper part of f. suprasylvia posterior, which results in a formation of a prominence raising as it were, the sinus venosus sagittalis superior.

The frontoparietal prominence is very strongly developed, causing the corresponding external convexity of the brain-case (fig. 4) on a level with f. lacerum anterius.

The temporal lobe is striking for its strong development and for the growth in the ventral direction, quite unusual in mustelids, but observed among Carnivores in bears. This phenomenon leads to a marked covering of the brain stem on the ventral side, and covering of f. rhinalis over a considerable length. This strong development of the temporal lobe, together with the formation of

the parietal protuberance makes the occipital part of the cerebrum of *Perunium* as high as in the bear, in distinction from the wide and low brain of mustelids.

There are four distinct convolutions as in bears.

The temporal and occipital lobes conceal to a considerable degree from the sides the cerebellum separated from the hemispheres by a well-developed tentorium.

Vessels. On the lateral surface two branches of a. meningealis media have been preserved, rising from the base of the hemisphere dorsally, one of them may be traced as far as the fissura coronalis, the other rises up to the lateral surface of the frontoparietal prominence, where it crosses the anterior end of the sagittal convolution at its junction with the praecruciform convolution, runs further up along the ventral end of the cruciform fissure and may be traced to the level of the apex of the Sylvian convolution. Along the medial line a wide cast of the sinus sagittalis parietalis is well preserved traceable as far as the occipital border of the brain, perceptibly swollen and receiving the lateral branches on a level with the cruciform fissure. The average width of the sinus is 2.3—3 mm.

The posterior border of the temporal lobe is sharply inflected medially. For dimensions of cerebrum see table 6.

Fissures of the cerebral hemispheres. In the following description I use the term "fissura", without distinguishing "fissura" and "sulcus", since the two terms are somewhat vaguely used in the literature on the brain of Carnivora. Likewise conventional are the indications to the apparent "depth" of the fissures, which certainly do not precisely render the true depth. For the sake of brevity I use the term "brain" instead of "cast of brain".

1. Fissura rhinalis Wilder is visible only in front of f. Sylvii: the remaining part is concealed by the temporal lobe.

2. Fissura Sylvii Kappers (f. pseudosylvia Bolk) is deep, long, its anterior end begins from f. rhinalis. It runs dorsally and obliquely backward. The shortest distance of the posterior end from f. suprasylvia is 11 mm, from the posterior border of the occipital lobe, 33.8 mm. The length of f. Sylvii is 22 mm, the greatest depth is at its junction with f. rhinalis. Towards its end the fissure gradually comes out to the surface of the cast. It has no branches except for r. temporalis, arising from the initial part of f. Sylvii and running below the gyrus reuniens (posterior) on the lower border of the external surface of the temporal lobe. The length of this branch is 12 mm.

3. Fissura cruciata Leuret is deep and, as is typical of martens and bears (KRUEG), long. It arises laterally at an angle of 45° from the medial border of the hemisphere on a level with the lower anterior end of the temporal lobe, and after a distance of over one centimeter runs laterally and even slightly backwards over a distance of about 20 mm, descending along the lateral wall of the hemisphere; then it curves slightly to the front. The length is 33 mm. At the

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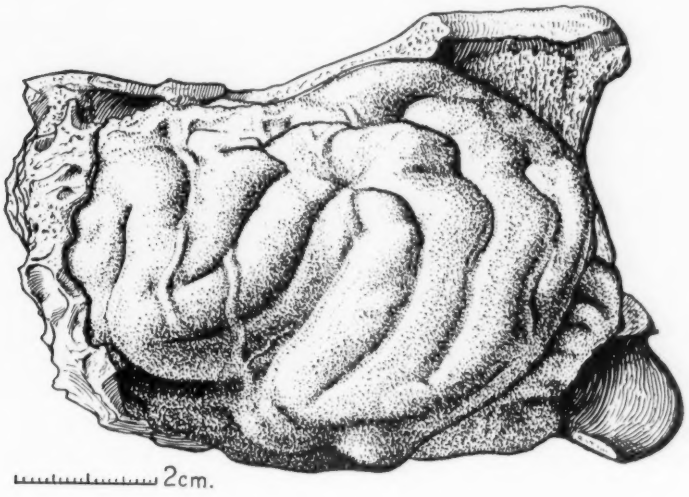
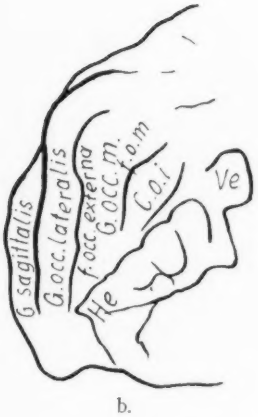


a.



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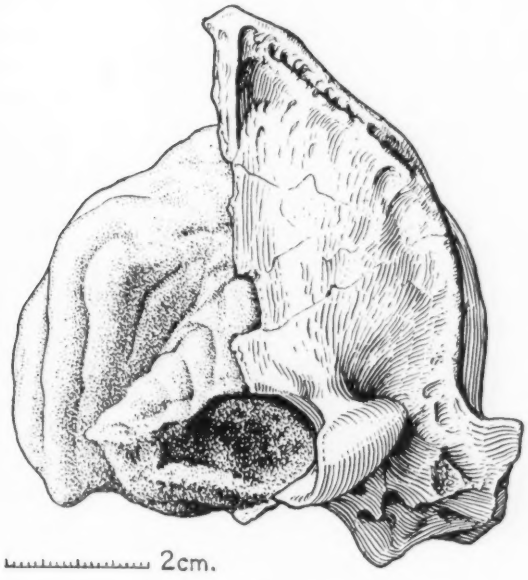

c.

Fig. 9. *Perunium ursogulo gen. et sp.n.* Endocranial cast of the skull No. 268. a.—left lateral surface. The convolutions and the branches of the middle meningeal artery are especially well defined. The anterior branch traverses the fore end of the gyrus parietalis and runs into the f. cruciata; the posterior branch gives off a lateral branch that reaches the f. sylvii, traverses the lower parts of g. sylvii and g. parietalis and reaches the f. coronalis (see fig. 9). b.—scheme of the fig. 9 c. c.—occipital view. Grebeniki. × 1.

first inflexion of the fissure, a short fissure (f. praecruciata) originates, directed medially and slightly forward, and disappearing under the cast of the sagittal venous sinus.

4. Fissura praecruciata Krueg is fused with the preceding one and runs forward and medially, forming with it an angle of about 35°. A small triangular convolution between these two fissures is covered from above by the lateral branch of the sagittal sinus widened at this place, and is much deeper in position than the adjoining convolutions. The two triangular convolutions of the right and left hemispheres formed evidently a rhomb (Ursine lozenge, MIVART) so typical of bears and large mustelids. The length of the fissure is 12.3 mm.

5. Fissura postcruciata Krueg is not developed as an independent fissure, at least on the cast. Possibly it is fused with the branches of f. ansata. F. postcruciata is observed in the badger and in the marten, although in the latter it is sometimes connected with f. ansata.

Caudally from f. cruciata two long fissures are present characteristic of Carnivora, encircling the Sylvian fissure and resulting each from a fusion of several fissures. The nearest to the Sylvian fissure is f. suprasylvia Owen; it may be subdivided into three parts, as follows.

6. Fissura suprasylvia anterior Flatau et Jacobson runs nearer to the Silvian fissure than does the posterior one, and is only slightly marked on the cast. The anterior end lies at a distance of about 10 mm dorsally from f. rhinalis and is nearly horizontal. The fissure gradually rises backwards, forming an arch concave forward and passing over the dorsal end of the Sylvian fissure into:

7. Fissura suprasylvia media Fl. et Jac., a short archlike fissure. From it two short secondary fissures branch dorsally, one 7 mm long, directed forward, the other 10 mm long, backward.

8. Fissura suprasylvia posterior Krueg is deep; slightly winding it runs behind f. sylvia ventrally, then turns obliquely downward and forward, forming an arch convex backward and downward. The lower end lies at a distance of 13 mm from the ventral border of the temporal lobe. The length of f. suprasylvia is 83 mm; f. suprasylvia media has the greatest depth, about 4 mm.

The next fissure between the above-described and the medial border of the hemisphere is a product of fusion of: f. coronalis, f. ansata, f. lateralis and f. ectolateralis. In small carnivores, possessing the least divided surface of the cerebrum, only f. lateralis is present, which appears in the ontogeny of large carnivores before the other three, and is phylogenetically the oldest.

9. Fissura coronalis Owen is the anterior part of this arched large fissure. Its anterior end lies in front of f. cruciata on the frontoparietal prominence at a distance of 12 mm from f. praesylvia. Hence f. coronalis, winding slightly, runs backward and after that up—and backward. Then it bends steeply forward and passes, as in all mustelids with the exception of the otter, into:

10. Fissure ansata Krueg. This short fissure forms an arch concave posteriorly. From its convexity three short branches originate, forming thus a Y. The first, lower, branch formes an arch, 11 mm long, convex ventrally, directed forward. The second is straight and runs forward and slightly upward including possibly elements of f. postcruciata (see above). The third is straight, 11 mm long, and runs dorsally. The points of origin of the three branches are separated from each other by intervals of 9 mm. The branches become shallow at their terminations.

11. Fissura lateralis Owen is the median horizontal part of the second arched fissure, beginning from the point of origin of the 3rd branch of f. ansata, and ending at the point of origin of the medio-posterior "branch", evidently corresponding to f. medialateralis (see below). The length is 16.5 mm.

12. Fissura medilateralis Owen (?). A medio-posterior "branch" of the 2nd arched fissure is a homologue of f. medilateralis as developed in the brain of bears. It is distinct in its initial part only and seems to have extend towards the occiput more or less parallel to the medial border of the hemisphere.

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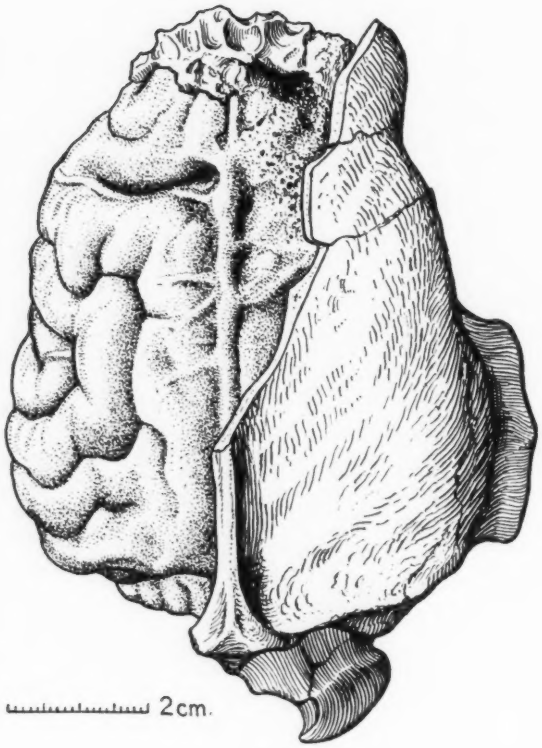
13. Fissura ectolateralis Wilder. FLATAU and JACOBSON (1899) designate, in the badger, the downward continuation of f. lateralis, as the "sulcus medilateralis". This is not correct, since according to KRUEG's data (1880), f. medilateralis in mustelids is never connected with the lateral fissure (it is present only in large species); this connection is rather characteristic of Canidae. Of martens and bears are characteristic: 1) an almost invariable presence of the ectolateral fissure; 2) its frequent junction with the lateral fissure. Therefore, I designate this continuation of the lateral fissure as f. ectolateralis and not medilateralis.

From the point of origin of f. medilateralis the ectolateral fissure runs downwards, forming an arch convex backward, then gives off forward a short (3 mm) branch. In its further sinuous downward course it follows f. suprasylvia posterior and reaches the ventral border of the lateral surface of the temporal lobe. The total length of the 2nd arched fissure is 120 mm.

14. Fissura paroccipitalis. Caudally of and parallel to the ectolateral fissure lies a deep fissure, probably corresponding to an analogous fissure on the brown and polar bear; it would be useful to give this fissure, due to its definite location, a special name, f. paroccipitalis. Its length is 37 mm. Ventrally of it there is a narrow fisure 20 mm long, lacking any connection with the adjacent ones and reaching the lower prominent end of the temporal lobe. The dorsal end of the paroccipital fissure comes out to the surface of the brain into a shallow depression, in which it is difficult to establish the course of the fissure.

A quite small fissure is discernible near the occipital border of the hemisphere, behind this depression.

15. Fissura praesylvia Owen (f. orbitalis). A distinct deep fissure; it begins from f. rhinalis anterior and rises up the anterolateral surface of the hemi-



a.

Fig. 10. *Perunium ursogulo gen. et sp.n.* Endocranial cast (the skull No. 268). a.—dorsal view (for explanation see fig. 8). b.—ventral view (for abbrevation see also fig. 2). Grebeniki. × 1.

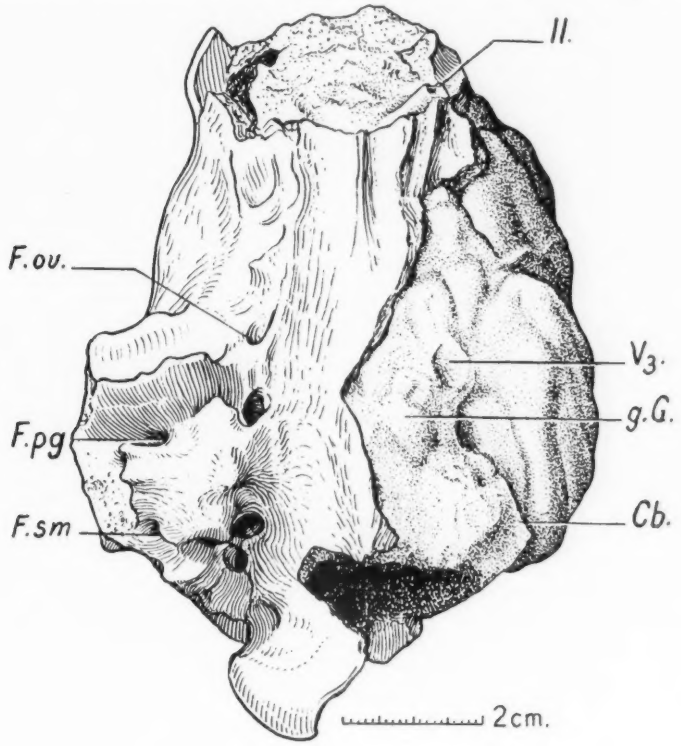
sphere, separating the frontoparietal prominence from the frontal lobe. The fissure runs round the frontal lobe upwards and slightly laterally, then slightly medially and more or less parallel to the distal part of the cruciform fissure. The length is 18 mm.

16. Fissura olfactoria. A short portion of it (3—4 mm) is seen in front of f. praesylvia, being directed towards the latter. It is an evidence of the proximity of the olfactory lobe from the boundary from which begins f. olfactoria.

17. Fissura prorea Krueg. Discernible is its posterior end which is parallel to the medial border of the hemisphere and is placed approximately on the level of the origin af f. praecruciata from f. cruciata.

The following fissures of the occipital lobe are seen when viewed from behind.

18. Fissura occipitalis externa, a long, gently sinuous fissure; it delimits from the medial side the lateral occipital convolution, delimited laterally by f.



b.

paroccipitalis. The upper half of the fissure rises from the lateral border of the tentorium at first nearly vertically and is deepest in the two lower thirds of its length. Higher up it describes a semicircle and terminates at a distance of 4 mm from f. occipitalis interna. The lower half is shallower, and descends, forming a gentle arch, from the lateral border of the tentorium towards the base of the temporal lobe as far as the level of the lower end of the Sylvian fissure. The basicranial end of the fissure curves sharply medially round the ventral end of the middle occipital gyrus.

19. Fissura occipitalis interna. It is a small fissure on the posterior surface of the hemisphere, bent at an obtuse angle open towards the tentorium. The length of the visible portion is about 20 mm.

Cerebral convolutions. 1. Gyrus Sylvii is rather long, encircling the Sylvian fissure. The anterior, narrower, portion seems to have been slightly overlapped in front by the parietal gyrus. The posterior wide part bears two more or less horizontal depressions, the upper one of which is deeper and more distinct than the lower. In its lower ends the convolution passes into the next, parietal convolution.

2. Gyrus parietalis embraces the gyrus Sylvii, being separated from it by f. suprasylvia and from the sagittal convolution, by the 2nd arched fissure. It is much longer and more complex than g. Sylvii, its horizontal part is wide, parallel to the sagittal suture. The surface is uneven, with irregular depressions, the majority of which, at least the larger ones, correspond to natural depressions on the cortex surface, resp. to prominences on the inner side of the parietal.

3. Gyrus sagittalis, embracing the preceding ones, is still longer, wider and more complex. Its anterior end is connected in the region of the frontoparietal prominence with g. parietalis and g. praecruciatus. The ascending portion, or g. postcruciatus is much wider than the parietal convolution, bears distinct depressions caused by the two first branches of f. ansata, and forms a strong convexity on a level with the lower part of f. cruciata. The middle part, parallel to the medial border of the hemisphere, is encircled anteriorly by f. cruciata and bears depressions caused by the 3rd branch of f. ansata and the f. medilateralis. On the level of the latter, the parietal part of the brain forms a dorsal longitudinal protuberance at the expense of this middle part of g. sagittalis. This protuberance imparts to the brain of *Perunium* a quite peculiar appearance, clearly different from all the known mustelids. The posterior part bears a wide shallow depression, from which f. paroccipitalis begins, absent in other mustelids, but occurring in bears; this latter calls forth a separation of a new convolution from the caudal end of g. sagittalis, single in other martens.

4. Gyrus occipitalis lateralis. It is an S-shaped convolution running where the lateral surface of the hemisphere passes into the occipital one. The upper end, directed towards the medial side of the hemisphere, is bent stronger than the lower one, which passes gently into the temporal lobe. The middle part, unlike the anterior convolutions, is distinct and narrower. Medially from it, on the posterior surface of the hemisphere, lies the:

5. Gyrus occipitalis medius, separated by f. occipitalis externa from the preceding, and by f. o. interna, from the next convolution. The dorsal wide end projects slightly backwards, beyond the level of the upper part of g. o. lateralis, and is therefore visible when viewing from the lateral side, in spite of the concave shape of the occipital end of the hemisphere, while the ventral end dives forward reaching the tentorium and is not visible from the side.

6. Gyrus occipitalis internus is small, and, like the preceding, fused with the occipital end of the sagittal convolution with its upper end; the lower end is fused with g. o. medius directly above the tentorium.

7. Gyrus praecruciatus (g. cruciatus anterior) runs round f. praesylvia and bears depressions from the short f. prorea and f. olfactoria.

The c e r e b e l l u m is separated from the cerebrum by an osseous tentorium, that penetrates rather deeply into the transverse cerebral fissure. The matrix filling the portion of the brain cavity, corresponding to foramen

occipitale magnum, flocculi, lobus posterior vermis, the ventral part of lobus paramedianus (tonsilla Ingvar) and the lower part of lobus ansiformis, is absent. The remaining parts, however, give an idea of the dimensions and the nature of the cerebellum.

The cerebellum is well developed; its proportions are in general characteristic of Mustelidae, but when compared to *Martes*, e.g., it is relatively small. The latter fact, however, by no means may be accounted for by a weak development of the cerebellum itself, but by the unusually large—for mustelids—volume of the cerebrum.

Vermis. Lobus anterior (Bolk, Ingvar) dives under the tentorium and is not visible. Lobus medius (Ingvar) is shaped characteristically of carnivores, bilaterally symmetrical, strongly convex behind, causing the strong vertical external convexity of the supraoccipital. The width of the external part of the middle lobe is 11 mm. Forward the middle lobe widens, especially in the upper part. The shallow sulcus paramedianus separates the middle lobe from the hemispheres, that reach far down and forward under the overhanging cerebral hemispheres. The lateral part of Crus II bears distinct traces of transverse fissures. The transverse fissures of the vermis seem not to be imprinted on the internal surface of the occipital bone; therefore the cast surface is smooth.

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The hemispheres seem to have been well developed, but are to a considerable extent covered by the occipital lobes of the cerebrum. In its proportions the cerebellum was like that of martens but not of bears.

The base of the brain may be but partly examined. Noteworthy is the strong development in the ventral direction of the temporal lobe which is quite unusual for the mustelids: the temporal lobe covers a large part of the rhinencephalon and extends medially beyond the level of f. ovale. Judging from the grooves present, there must have been fissures on its ventral side. One of the grooves runs towards the base of f. Sylvii and corresponds to a similar fissure in bears. Medially of it lies another, more or less longitudinal one. The ventral part of the temporal lobe extends forward to the level of f. lacerum anterius. The postero-ventral border projects downwards forming a prominence into which passes the ventral end of G. occipitalis lateralis. On the level with this prominence, and adjoining postero-medially the oval foramen, and covering the interspace between Pons Varolii and the base of the temporal lobe resp. pedunculus of the cerebrum to the Pons, there lies an anteriorly expanded protuberance, evidently a large semilunar ganglion (V).Pons Varolii is rather feebly convex ventrally.

The b r a i n r e l i e f and the e x t e r n a l s u r f a c e of the brain-case (fig. 11). The growth of the brain in small mammals, of Carnivores most markedly in martens, causes the formation of depressions on the inner surface of cranial bones in a greater degree than in large animals. Sometimes the rate of growth of some parts of brain is greater than the increase of the volume of

the brain-case; in some cases this increase seems to come to an end before the growth of the brain has been completed. Then, under the pressure of the brain, not only the "impressiones digitates" and the crest-like juga cerebralia are formed, but also, following a strong thinning of the wall of the brain case, convexities on the external side of the bones are developed. In the relief of the outer side of the brain-case some elements of the relief of the brain itself may be recognized. In *Perunium* we distinguish:

1. Prominentia frontoparietalis is formed mainly by the anterior end of g. parietalis, at its junction with g. Sylvii and g. sagittalis. This prominence is bounded ventrally by a shallow depression, corresponding to the lower border of f. Sylvii, but not directly to f. rhinalis anterior. The latter lies here on the level with the medial border of f. lacerum anterius.

2. P. fronto-parietalis passes dorsally and slightly backwards into a small elongated elevation, apperently corresponding to the strongly convex part of g. parietalis approaching f. cruciata.

3. Fissure of Sylvius is distinctly reflected in a large depression on the lateral wall of the skull in the temporal fossa.

4. To the four convolutions of the temporal lobe (g. sylvii, g. parietalis, g. sagittalis and g. occipitalis lateralis) four parallel arched ridges correspond divided by faint grooves.

5. The anterior end of the temporal lobe on the level of the base of f. sylvii produces a prominence on the posterior side of the Sylvian depression above the base of the anterior border of the temporal arch and the oval foramen.

6. On the occipital side of the skull the vermis of the cerebellum causes the development not only of fossetta vermiana (ALBRECHT 1884), but also of a "prominentia vermiana" on the external surface of the much thinned squama of the occipital bone, as in the living *Martes*.

Prominentia parietalis, formed by the growth of the sagittal convolutions in the dorsal direction causes a thinning of the wall of the parietals thickened by the sagittal crest, this results in a weakening of the base of the crest, but is hardly reflected on the external relief of the parietals.

Comparison of the brain of Perunium with that of the recent and fossil mustelids and other carnivores. The cerebrum of *Perunium* differs from that of all mustelids not only in its large size, which is quite natural in such a large animal, but also in large dimensions of the temporal, occipital and parietal lobes. The brain is thus much more like that of bears, especially of the polar bear, than is common for mustelids. This resemblance is pronounced, 1) in the presence of three fissures and four convolutions on the temporo-occipital part of hemisphere, as in bears, instead of two fissures and three convolutions of martens; 2) in a complex subdivision of the postero-medial angle of the cerebrum; 3) in the considerable height of the posterior half of the hemisphere, which is undoubtedly the principal cause of the resemblance of the

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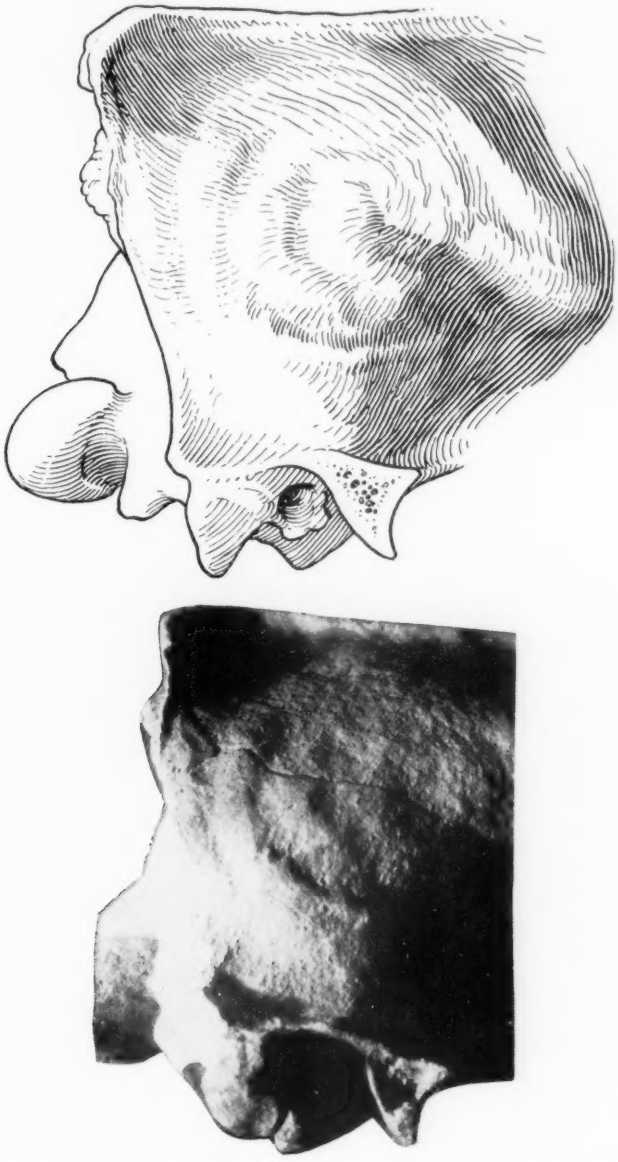

Fig. 11. *Perunium ursogulo gen. et sp.n.* The outer side of the brain-case of the skull No. 268. The convolutions of the temporal lobe are well defined on the outside of the brain-case. For explanation see the text and fig. 8. Grebeniki. × 1.

occipital part of the brain-case of *Perunium* to that of bears; 4) in the strong development of the occipital convolutions. However, the cerebrum of *Perunium* is built after the pattern common for martens, rather than after that common

for bears. In fact, in *Perunium* f. sylvii is shorter and more oblique than in bears, the pre- and postsylvian of gyrus Sylvii embracing the f. Sylvii are less closely spaced than in bears, although more closely so than in smaller mustelids.

The cerebellum squeezed into a wide depression on the posterior side of the cerebrum likewise has a shape characteristic of mustelids, and not of Ursidae. On the other hand, the deep f. paroccipitalis, the strongly projecting g. occipitalis lateralis, the strong development of fissures and convolutions on the occipital border of the hemispheres, the enormous development of the sagittal convolution in the parietal region and the ventral growth of the temporal lobe, clearly distinguish the cerebrum of *Perunium* from that of all other mustelids. Leaving aside the peculiar feature, namely the parietal prominence, the cerebrum of *Perunium* is the ultimate member of a series which may be constructed by arranging in the order of increasing complexity the brains of different mustelids, from the smallest ones, like *Mustela vulgaris*, to the glutton and *Perunium*. Thus, there are reasons to believe that the mixture of features of martens and bears in the cerebrum of *Perunium* is due not so much to its kinship to bears, as to convergence. On the other hand, the resemblance to Ursidae was noted above in the structure of the skull: 1) in the disposition and direction of the foramina for nerves II, III, IV, V and VI, and 2) in the structure of the orbito-temporal crest. All this makes us regard convergence as the sole reasonable resemblance with some reserve.

In the structure of its brain *Perunium* stands quite apart among all other mustelids in even greater degree than in the skull structure.

Of all recent Arctoidea s.l. only the brain of dogs was subjected to a detailed experimental study. Therefore, we can judge about the brain of *Perunium* only on the basis of data obtained for dogs. The following may be noted:

1. One of the features of the cerebrum of *Perunium* as compared to *Martes, Meles, Gulo* etc., is the great development of the temporal lobe, which should be in accordance with some peculiarities in the differentiation of the psycho-auditory region of the cortex.

2. The strong development of the occipital lobe affords evidence of a certain specific differentiation of the optical psycho-sensorial region.

It is the temporal lobe of mammals which is characterized by the greatest diversity in the internal structure of the gray matter; this is probably an evidence of a great diversity in the differentiation of the hearing. The progressive development of the temporal lobe is characteristic of definite stages in the evolution of primates, of Man in particular. It seems that the succession of "progressive cerebration" in this latter case is such that the development of the auditory area precedes and stimulates the progress of the frontal lobes. In *Perunium*, however, we have a case of some specific differentiation of hearing, unknown to us, without any perceptible correlative progress of frontal lobes. An analogous instance we possibly have in the case of bears.

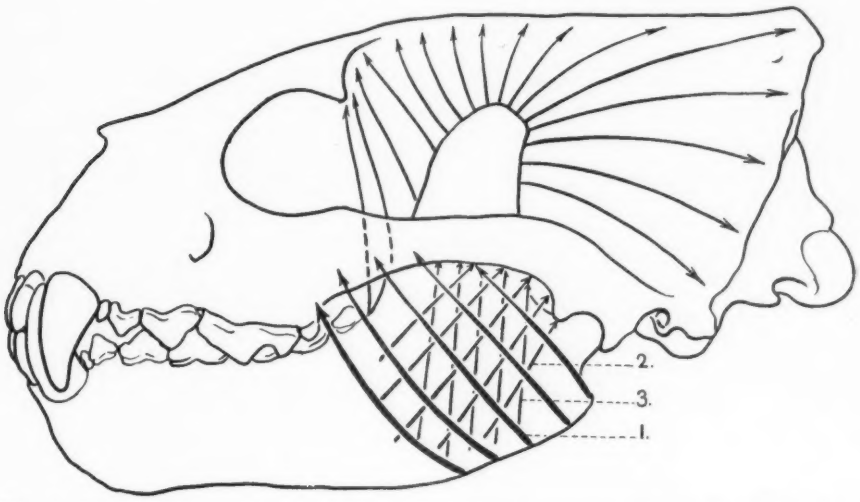

Fig. 12. *Perunium ursogulo gen. et sp.n.* Diagrammatic representation of the distribution and direction of the muscular fibres of the m. temporalis and of the external, medial and internal (1—3) layers of m. masseter. Diminished.

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Unfortunately we have no data on the internal structure of the grey matter either for *Perunium* or even recent bears and martens. Thus the most reserved "roundabout" considerations are as yet impossible.

SOME DATA ON THE SKULL CONSTRUCTION AND THE JAW MECHANISM.

I have had no material for preparation of muscles of head of large mustelids, therefore the below considerations had to be based on litterary data.

The following features are characteristic of *Perunium*: 1) Low position of the gently sloping, slender zygomatic arch, with a low set articulation. 2) A weak sagittal crest. 3) A short facial part, with a considerable height both of it and of the mandible. 4) Rather thin lateral walls of the brain-case with an early obliteration of the sutures. 5) A relative weakness of the dentition of a carnivorous type.

Let us consider the most essential points.

1. The superficial layer of m. masseter begins from the anterior part of the zygomatic arch and is attached to the mandibular angle. The middle layer originates from the posterior third of the arch and terminates on the lateral side along the posterior part of the ventral border of the fossa masseterica. The inner layer begins from the postero-ventral and medial side of the zygomatic arch and terminates on the lateral side in the fossa masseterica. When the zygomatic arch is high and strongly convex upward, the contraction

of each of these layers may be split into two main component forces, one raising the upper jaw, the other imparting a forward or backward movement. The third action of m. masseter drags the mandible laterally. In case of *Perunium,* with a low and thin zygomatic arch, the force of m. masseter, raising the mandible and pressing the teeth together, was less than it might be expected in so large a skull. The antero-posterior movement of the mandible, since mobility of the ginglymal jaw articulation was limited, must have been auxiliary to the cutting action of $\frac{P^4}{M_1}$ $\left(\text{to a lesser degree } \frac{M^1}{\text{talonid } M_1}\right)$ rather than "chewing". From the low position and great lateral convexity of the zygomatic arch in *Perunium* follows that a considerable part of fibers of m. masseter, especially of its middle and internal layers, must have drawn the mandible laterally. In contracting simultaneously the right and left masseters (in catching a prey), this sidewise action was neutralized; while the increased strain of the masseter of one side must have pressed with force the mandible teeth against the inner side of the upper dentition i.e. the upper and lower shearing teeth acted as halves of strong scissors.

The jaw articulation of *Perunium* is low, on a level with the crowns of the upper teeth. In forms with a high position of the articulation (ungulates, rodents), the trajectory described by the crown surfaces of the lower teeth is such, that the food is slightly pushed forward. In forms with a low position of the jaw articulation (*Smilodon*) the trajectory of the crowns of the lower teeth is such that the food is slightly pushed backward, and thus bringing jaws together assists swallowing. Apparently the same case we have in *Perunium.*

2. The jaw apparatus of *Perunium* was therefore "seizing" and not "chewing". We should expect strong m. temporalis and sagittal crest in so large a skull. But the sagittal crest in *Perunium* is weak.

The high spacious occiput of *Perunium* with a long transverse crest forms a large area for the posterior third of m. temporalis, terminating on the posterior half of the coronoid process. Judging by the size of the posterior half of the brain-case of *Perunium,* the strength of this part of m. temporalis, drawing the mandible, must have been great; great should have been also both the rapidity in shutting the mouth and the resistance to dislocation of the mandibular condyles out of joint by the struggle of the prey. Such a strong development of the posterior part of the temporal muscle might, to a certain extent, compensate a possible relative "weakness" of the middle third, originating on a level with and on the sagittal crest.

3. It is possible, that this strength in shutting the jaws is associated with the considerable height of the mandibular rami and of the snout. The teeth being relatively small and of a carnivorous type, it would be difficult to explain this height of the jaws by an adaptation to crushing of bones. A high but narrow body of the mandible we meet in carnivores with grasping and tearing "habits",

e.g. in Gorgonopsia among reptiles. In any case, the considerable height of the snout of *Perunium* suggests a heavy stress upon the symphysis and its antagonists the intermaxillaries and the anterior ends of maxillaries.

The pterygoids have been broken away, this prevents us from forming a correct idea of the nature of work of m. m. pterygoidei.

4. The lateral walls of the brain-case are thin. The sagittal crest is weak. It seems that in *Perunium*, in spite of its size, the brain-case is to a certain extent of the same type as in small-sized martens, the skull of which is deprived of the sagittal crest but bears well-developed juga cerebralia.

The mechanical importance of the juga, as well as of the entire internal compact lamina in the skull of mammals, of carnivores in particular, to my knowledge has so far been underestimated. Yet it is very great even in the thick-walled skull of the bear. Especially important is the strength of the entire vault of the brain-case as a whole in animals with a thin-walled brain-case. Just in small carnivores the juga are rather strong, projecting deeply into brain fissures. They embrace in an arch-like manner jugum Sylvii entering f. Sylvii; after the fissures, into which they project, these main juga may be named the jugum suprasylvium and the jugum laterale. In small martens the main juga form, as it were, buttresses of the brain-case reinforcing its lateral wall from within. Of these, j. Sylvii is so oriented as if it were following the "resultant" of the whole m. temporalis, while j. suprasylvium and j. laterale supplement this buttress. Such arch-like juga obviously must be strongly developed in small- and medium-sized carnivores with a strong m. temporalis—martens, cats, etc.—but are relatively weak in 1) mammals with a predominance of m. masseter (herbivores, bears) and 2) in large animals with a thick-walled brain-case, and in particular with a pneumatized one (cave bear, elephants, etc.).

A question arises as to wether the course of the fissures depends upon the position of the juga cerebralia. We may only note here 1) the mechanical importance of juga in the brain-case of small carnivores; 2) the possibility of a certain significance of the development of juga in the origin of the cerebrum relief, in general being of a very similar type in different carnivores.

It is possible that just the weakness of m. temporalis, together with the great development of m. masseter and hence quite different mechanics of the brain-case play a certain part in the eveness of the hemispheres in rodents, even in large ones.

The above said, certainly, should not be understood in a sense that the mechanical stress upon the brain-case is the only cause of the development of the internal relief of the brain-case, and, secondarily, of the brain relief. On the contrary, it is known that the action may be reverse, so that in the external relief of the brain-case some convolutions of the brain may be recognized (see above).

Nevertheless, both cerebral juga enumerated above, and jugum cruciatum of

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carnivores, along with the tentorium and the occipital juga, form a system of internal buttresses of the brain-case. The mechanical importance of these structures will evidently lessen with an increase in the animal's size and in the thickness of the wall of its brain-case, with its pneumatization, with a release of pressure upon the brain-case following a strong development of m. masseter and a reduction of m. temporalis; as a result the juga, as well as the impressiones digitatae, will be but slightly developed, and the inner relief of the brain-case will by no means reveal the richness of the brain in convolutions and fissures, and a cast may give a false idea of an "eveness" of the brain.

As is known, the Sylvian fossa is formed early and in any case long before the jaw muscles begin to function, and the jaws themselves are completely formed. Thus, there can be no influence of the bones upon the formation of the Sylvian fossa and fissure in the early embryogeny of recent mammals. However, this does not exclude such influence in phylogeny or at later stages of ontogeny, when the tone of muscles appears. If at the beginning of ontogeny the formation of the brain-case in mammals is subject in the greatest degree to the influence of the developing cerebrum, at later, post embryonic stages, the brain itself is limited by the brain-case, although the latter does enlarge before sutures and fontanels are obliterated. After the onset of mechanical stress upon the brain, it cannot but meet, although indirectly, structures like the tentorium and the juga. The formation of the latter may be "passive", as a result of the formation of deep impressions on the inner surface of the skull during resorption under the pressure of developing convolutions; the possibility is not however excluded that at early stages of evolution a reverse influence took place, apart from a later "adaptation" of the brain-case and its juga to the shape of convolutions and fissures. An indirect evidence of the possibility of such an assumption is afforded by the variability of the arrangement of BRODMAN'S fields and the lack of an accurate correspondence in the topography of these, on the one hand, and of fissures—on the other. From this standpoint the appearance of a "Sylvian" fissure might be expected already in reptiles with a predominance of m. temporalis.

With an increase in size of the skull and its strength, the rôle of the juga may become quite small, and the shaping of the cerebral relief will be free from the influence of the internal relief of the skull, and only the reverse influence, of the brain upon the skull, will remain. In descendants of the creodonts, e.g. in ungulates, the relief of the brain may develop in a way different from the carnivores, and retain only the principal features (f. Sylvii, f. cruciata, etc.). Free from the restraining effect of the juga, the relief of the cortex in proboscideans, aiming at a maximum accumulation of principal elements of the grey matter in the least possible volume, possesses the strongest folding, the details of which are difficult to compare with those in other mammals.

The brain-case of *Perunium* is lacking any strong sagittal crest. This feature

Fig. 13. *Perunium ursogulo* ORLOV. Reconstruction, made by C. C. FLEROW.

is probably in correlation with the slight development of the facial part, of the canines in particular. On the other hand a study of a sagittal section of a bear skull shows that the pressure transmitted on the sagittal crest from the upper canines and incisors does not trend entirely towards the occipital crest, as figured by MARINELLI (1931, 1939), but is dispersed, being transmitted on the lamina vitrea and its juga. Some "juga" of a brain-case like that of small carnivores must be oriented in accordance with the task—to offer resistance not only to compression caused by the work of the temporal muscle, but also to that caused by an impact received at once from the front (in seizing the prey) and from behind (by the load of the body of the animal).

In addition to a system of beams in the frontal cavities and the mentioned juga, to the strength of the anterior part of the brain-case contribute the cruciform and praesylvian juga, and the orbito-temporal crest.

MODE OF LIFE AND CAUSES OF EXTINCTION.

Cannot yet be convincingly elucidated due to the absence of the postcranial skeleton. Our assumptions are based only on the skull and brain of *Perunium*, the dention of *Eomellivora* and *Perunium*.

The large size, the carnivorous teeth, along with blood-thirstiness common of almost all mustelids, undoubtedly made *Perunium* dangerous not only for small animals but also for the majority of the ungulates.

A comparison of the skull and teeth of *Perunium* with those of the glutton shows that gluttons have a more powerful facial part, thicker crushing teeth, and a more powerful zygomatic arch, a strong sagittal crest, projecting far backwards, stronger jaw muscles, etc. *Perunium* in all these features is a less specialized animal.

The character of the teeth of Peruniinae indicates their mainly carnivorous mode of life; this is substantiated by the comparison of $\frac{P^4}{M_1}$ and $\frac{M^1}{M_2}$ with the corresponding teeth of mustelids of a more "omnivorous" type (*Meles, Taxidea, Arctonyx,* and their extinct relatives). M_1 of *Perunium* has no metaconid; its proto- and paraconid are rather blade-shaped, and while the length of the blade is great as compared to *Gulo*, they are weaker and narrower than those of the smaller-sized *Gulo*. The talonid of M_1 in Peruniinae, unlike the cup-shaped and many-cusped talonid of the omnivorous forms, is a simple longitudinal crest, functioning as a blade though obtuse. Unlike the blade of the anterior greater part of the tooth constituted by the proto- and paraconide and functioning like scissors, the longitudinally elongated talonid of M_1 has its antagonist in the shape of a large transverely elongated M^1, much resembling that of *Martes*.

Perunium and *Eomellivora* are divergently evolved generally, the teeth of *Perunium* being more specialized and more carnivorous than those of *Eomellivora*, the latter being possibly more omnivorous. These differences in the mode of feeding and nature of the prey may account for the probable co-existence of these animals.

The relatively weak prae- and postglenoides of *Perunium* indicate a small (as compared to *Gulo*, e.g.) antero-posterior stress of the trochlea of the lower jaw in the glenoid fossa, and hence, also, a relative weakness of m. masseter. This fact agrees with the relative weakness of the teeth of *Perunium* which are carnivorous, but not adapted for crushing of thick bones.

An indication of the relative weakness of the action of $\frac{P^4}{M_1}$ is furnished also by the low position of the jaw articulation. All this, as well as the small size of the canines, is a convincing evidence that the chief food of *Perunium*

must have consisted of rather small animals—rodents, insectivores, birds, lizards, frogs, possibly fishes.

Unlike the cerebrum, which is so "bear-like" in its temporal lobe, the cerebellum of *Perunium* is typical of mustelids. Like in *Gulo*, or in *Ictonyx* it seems to be squeezed into a depression formed by the concave posterior surface of the cerebrum. The relative sizes of the vermis and hemisphere likewise resemble those of martens and gluttons.

The anatomical and experimental data agree in that the vermis is the principal and oldest static organ of the cerebellum (palaeocerebellum), although not the only one, since this function in higher mammals is performed by the pallidostriatal system too. It is through the vermis that mass impulses come to the nucleus rubrum and motor centers of the tegmen. These data corroborate BOLK's scheme according to which the principal sphere of competence of vermis are: the muscles of the head, the jaws, the neck, breathing muscles, those of the trunk, and the tail. Here also is located the unpaired center of simultaneous work of the extremities. Thus the principal competence of the vermis is in the right and left skeletal muscles, working simultaneously, predominantly the trunk muscles.

The hemispheres of the cerebellum appeared later in evolution (neocerebellum) and are connected by pathways with the cerebrum (chiefly with its frontal lobes), being as it were a "superstructure" above the vermis; their growth was parallel to the increase of the communications of the cerebellum with the cerebrum, and their main competence is in the complex activity of the paired extremities.

In the light of these data it is interesting to note the strong development of the hemispheres of the cerebellum in *Perunium*. This is an evidence of the dexterity and agility of the animal just in using the paired extremities. Periniinae, in spite of their large size, retained probably the capacity of climbing trees in even greater degree than e.g. gluttons.

The cerebrum of *Perunium*, in spite of its large size and the high specialization of the parietal and temporal lobes, unusual for mustelids, shows primitive features: 1) the small size of the frontal lobes and the relatively weak development of the fissures of the frontal, frontoparietal and occipitoparietal region. According to the DARESTE and BAILLARD's law of progressive increase of complexity of the cerebral cortex with the increase of the size of the animal in the process of evolution, we should expect from the cerebrum of *Perunium* a much greater richness in additional fissures and convolutions than e.g. in *Martes* and *Meles*. However, in the much smaller *Martes* all the fissures of *Perunium* are present on the lateral surface of the hemispheres except the paroccipital fissure (a certain suggestion of it in the shape of a long slight groove is found on the brain of *Martes* sp. in the Moscow Brain Institute).

The lateral surface of the cerebrum of the badger is perhaps richer in

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fissures and convolutions than in *Perunium;* in any case it holds true with the frontal lobe. This latter in *Perunium* is much less developed than the parietal, occipital, and especially temporal lobes, as compared to the badger. Of course, it may be only stated that the increase of volume of the parietal, occipital (sight) and especially temporal (hearing) lobes in *Perunium,* being essentially an increase of the "screen", or the region of the projection of perceptions from the outer world (with their treatment in the psychosensorial centres) was not accompanied, due to some reasons, by a corresponding "progressive cephalization" of the frontal lobes. This peculiar "disharmonious" specialization might have been one of the fatal moments in the destiny of Peruniinae. A sharp change of the enviroment e.g. in the conditions of prey hunting and in the composition of the prey must have been still more beyond the strength of *Perunium* than of the other large carnivores of the Hipparion fauna. Such a change clearly occurred in the Middle and Upper Pliocene, when the meadows and forest-steppes of the middle latitudes of Europe with a rich vegetation upon which numberless hipparions artiodactyls, rodents, and insectivores fed, were replaced by dry steppes and semideserts inhabited by camels, small rodents, etc. (SIMIONESCU 1930). Peruniinae, which probably were hunters of meadows and forests, under new conditions could not compete with carnivores like hyenas, foxes and jackals; in the more woody northern regions they were doomed to an unequal struggle for existence against smaller but more omnivorous gluttons and badgers. However, besides these causes of extinction of *Perunium,* other causes of a general nature are also possible, which led to the extinction of a number of interrelated animals of the Hipparion fauna, particularly of its numerous carnivores.

This paper was written, when I received the opportunity to acquaint myself with the interesting paper of JULIUS PIA (1940) describing fragmentary remains of a new genus *Hadrictis* (from the lower pliocene of Vienna) this genus being closely related to Eomellivora and was placed by the author together with some other fossil martens in a new subfamily *Ischyrictini.*

The author places *Eomellivora* together with *Mellivora* in the subfamily *Mellivorini.* In my opinion, it is the same mistake which was made by O. ZDANSKY and G. E. PILGRIM.

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GAMETOGENESI E STRUTTURA ISTOLOGICA DELLA GONADE IN CHIRONOMUS THUMMI KIEFF.

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INTRODUZIONE.

I Chironomidi costituiscono un eccellente materiale di studio sia di cromosomologia (basti ricordare i cromosomi giganti delle glandole salivari e di altri epiteli di tali insetti), sia di embriologia (le loro uova sono tra le più trasparenti, di modo che si possono seguire nell'uovo vivente tutti gli stadi dello sviluppo). Ad eccezione però di AA. molto vecchi (ROBIN, WEISMANN, METSCHNIKOFF, KUPFFER, GRIMM, BALBIANI, JAWOROWSKY, RITTER, KOSCHEVNIKOFF, essenzialmente) che hanno studiato lo sviluppo embrionale delle cellule sessuali e l'evoluzione dell'ovario, nessuno ha rivolto l'attenzione a quella che è la fine struttura delle cellule sessuali e degli organi riproduttori in genere, uniche

ricerche in merito essendo quelle di carattere embriologico di HASPER [1] e quelle di cromosomologia di WOLF (1941) e di PHILIP (1942) [2] sulle modalità della meiosi in alcuni generi di Chironomidi.

Risultò quindi opportuno studiare e descrivere dettagliatamente la gonade allo stato di maturità sessuale, nonchè seguire la spermatogenesi e l'ovogenesi teneudo presenti l'aspetto morfologico e la sviluppo degli elementi maschili dallo stadio di spermatogonio a quello di spermatozoo maturo, cosa non fatta ancora da nessuno per questa famiglia di Ditteri.

MATERIALE E TECNICA.

La presente ricerca è stata eseguita su materiale di *Chironomus thummi* Kf., proveniente dagli immediati dintorni di Padova, più spesso allevato da uova in laboratorio. Si studiarono dal punto di vista della gametogenesi embrioni, larve, ninfe e adulti, sia ♂♂ che ♀♀. Avendo allestito degli allevamenti potevo prelevare periodicamente delle larve in successivi stadi di sviluppo onde ottenere una seriazione la più completa possibile per lo studio della maturità sessuale.

Il materiale è stato fissato essenzialmente in Karpetschenko, solo in piccola parte in Ezra-Allen o in fissativo di Poulson modificato da HUETTNER (formalina 40 %, alcool 95°, acido acetico, in proporzione di 5:15:1, indicato particolarmente per l'embriologia della *Drosophila*; io lo ho usato specialmente per lo studio di gonadi indifferenziata).

Colorai generalmente coll'ematossilina de Heidenhain, solo per lo studio della struttura generale della gonade usai l'ematossilina di Mallory (o quella di Ehrlich) e l'eosina. Le sezioni furono tagliate a 5 μ (inclusione in paraffina).

STADIO DI GONADE INDIFFERENZIATA.

Le mie osservazioni cominciano dallo stadio in cui la gonade ha raggiunto la sede e la fisionomia che conserverà poi fino alle condizioni definitive di sviluppo, e le dimensioni di circa μ 34×71.

Per quelle che sono le condizioni della gonade negli stadi precedenti a quello da me investigato, osserverò solo per inciso che le prime cellule della linea germinale sono le cellule polari [3]. Queste sono delle cellule rotondeggianti, vesci-

[1] TALE, A. (1911) segue molto accuratamente, con criteri di studio moderni e con metodica adeguata, il destino delle cellule sessuali primitive fino alla formazione dell'organo sessuale nella vita larvale.

[2] Vedi anche SÉBESS (Arb. erst. Abt. Ung. biol. Forsch. inst., 5, 1932) citato da JOHANSSEN e BUTT.

[3] Le cellule polari («Pol-zellen» degli AA. tedeschi) sono state studiate esaurientemente dall'HASPER nel suo lavoro del 1911. Secondo tale A. dalle cellule polari si formano 8 cellule binucleate. Tale stadio rimane indi stabile, senza divisioni cellulari, per i successivi periodi embrionali. Nel periodo larvale la gonade rimane nel VI segmento addominale, al limite tra proctodeo e mesenteron. Entrambi i sincizi genitali si uniscono reciprocamente nella formazione della gonade e si circondano di cellule mesodermiche colla formazione di un epitelio. Indi si spostano fino all'VIII segmento. Esistono a tale stadio due sospensori da entrambi i lati della gonade.

colari, molto più grandi delle somatiche, presenti in numero da 2 a 5, e disposte ad un polo dell'uovo, esternamente alle cellule del blastoderma. In uno stadio successivo, contemporaneamente alla formazione dello stomodeo e del proctodeo (ectoderma), si ha l'immigrazione dei gonociti nella cavità primitiva del corpo, ed il raggruppamento degli stessi nell'organo sessuale, posta nella metà caudale dell'insetto, vicino all'estremità craniale del proctodeo. A tale stadio è presente ancora molto tuorlo. In un periodo posteriore si hanno gli abbozzi del tubo digerente, del sistema nervoso (molto sviluppato nella regione cefalica, gradatamente ristretto verso la regione caudale, e già abbozzato in struttura metamerica) e delle glandole salivari. In tale stadio la gonade è bene abbozzata e delimitata nettamente dalla regione circostante, costituita da un ammasso di cellule molto vicine le une alle altre, di cui riesco a contare circa 12 in una sezione di massimo diametro. Tali cellule hanno un nucleo vescicolare molto grande, più grande anche dei nuclei salivari, senza cromatina bene differenziata, tanto che si deve dedurre che in tali stadio non si ha moltiplicazione cellulare.

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Nello stadio da me investigato la gonade appare come un ammasso irregolare di cellule indifferenziate a forma di sacco fusiforme allungato, agli estremi craniale e caudale piuttosto acuminato, e tenuto in sito, oltre che dai corpi adiposi con cui contrae rapporti molto intimi, da due legamenti sospensori. Questi ultimi sono costituiti di una sostanza di tipo connettivale, in cui si possono osservare delle striature longitudinali poco nette, e che non presenta traccia di nuclei o di altre particolarità cellulari. Le dimensioni della gonade in tale stadio sono in media μ 34 × 71. Per quello che riguarda la costituzione dell'organo, si osserva esternamente una tunica propria cui aderiscono strettamente gli elementi germinali più periferici, senza alcuna differenziazione di epitelio germinativo vero e proprio. Lo strato peritoneale è rappresentato, in qualche preparato, da un foglietto con rari nuclei allungati aderentissimi alla tunica propria e dello spessore di circa 2 μ. Gli elementi germinali, protogoni e deutogoni, sono ammassati in modo uniforme in tutta la gonade senza alcuna differenziazione di nidi o di altre strutture anatomo-microscopiche. E' da notare sin d'ora che in qualche gonade di dimensioni maggiori (μ 63 × 156) si osserva un netto alone citoplasmatico intorno al nucleo.

I nuclei hanno contorno netto, rotondeggiante o leggermente irregolare, dimensioni medie μ 4,8. A volte vi si distingue un nucleolo. In alcune gonadi i nuclei sono tutti in riposo, in altre ancora un gran numero presenta dei segni più o meno evidenti di rimaneggiamento del materiale cromatinico, assumendo a volte una netta disposizione di profase. Nei nuclei a riposo (fig. 9 a) la cromatina è estremamente fine, diffusa piuttosto omogeneamente, senza condensazioni all'interno della membrana nucleare o qua e là nell'interno del nucleo stesso. Nei nuclei in profase (o in preparazione alla stessa) si notano dei filamenti cromatinici molto delicati (fig. 9 b), in qualche singolo caso più netti, che vanno da una parte all'altra del nucleo, incrociandosi con altri, senza alcuna

polarizzazione. Vi si possono distinguere i cromomeri. In qualche altro caso ancora si osservano degli addensamenti di cromatina molto spessi, scuri, irregolari, uniti o no da filamenti, spesso polarizzati verso un punto della parete nucleare. Talora i filamenti sono più spessi, scuri, e uniscono granuli grossolani. Nelle gonadi di dimensioni più piccole non osservo alcuna metafase, nè alcuno stadio successivo.

Ho già accennato a alcune gonadi le cui dimensioni superavano quelle medie riscontrate: in tale stadio la nota più caratteristica è la presenza di citoplasma bene differenziato in quasi ogni cellula, rappresentato da un alone perinucleare più o meno regolare, oppure asimmetrico, e tinto abbastanza decisamente in grigio (fig. 9 d). Le dimensioni di tali cellule sono molto variabili, andando da μ 3,5 a 7, in media 5 (nuclei da μ 3,5 a 6). In certi casi si notano degli elementi a contorno ovale. Gran parte di tali cellule sono in moltiplicazione, e precisamente quasi tutte in stadio di profase (filamenti cromosomici molto fini, disposti a gomitolo diffuso irregolarmente in seno al nucleo, senza alcuna polarizzazione o condensazione, contorno nucleare ancora ben conservato). Osservo un caso di metafase (fig. 9 c): il limite nucleo-citoplasmatico è scomparso; non riesco ferò a distinguere il fuso acromatico.

Notevole la presenza di numerosi granuli neri o grigio-scuro, perfettamenti rotondi, diffusi omogeneamente in tutta la gonade, di dimensioni da μ 1,5 in giù, raggiungendo raramente i μ 1,9. Non posso stabilire se si devono considerare extra- o intracellulari, tuttavia propendo a ritenerli intracellulari. Forse si possono interpretare come materiali di diserva di secrezione.

Degni di nota sono ancora degli elementi di tipo epiteliale, rotondeggianti o leggermente ovali, a materiale cromatinico condensato al centro del corpo cellulare, disposti alla periferia dell'organo e osservati in un solo esemplare. In certi punti della gonade formano quasi uno strato epiteliale. Interpreterei tali cellule, con qualche riserva, come elementi non strettamente germinali, di tipo epiteliale o stromatico.

SPERMATOGENESI.

CARATTERISTICHE GENERALI DELLA GONADE MASCHILE.

Il testicolo nel genere *Chironomus* è di tipo unifollicolare (o uniloculare). Le cellule germinali stanno riunite in nidi molto caratteristici (fig. 6), senza alcuna formazione di cisti (come è il caso per molti testicoli di Insetti), e senza una differenziazione di sostanza interstiziale (almeno non dimostrabile con la colorazione dell'ematossilina ferrica) o di altre peculiarità anatomo-microscopiche. L'assetto a nidi è presente fin dai primissimi stadi degli spermatociti I e si conserva, sebbene meno netto, fino allo stadio di spermatide.

Nelle sezioni da me esaminate non sono riuscito a cogliere il passaggio dalle condizioni di gonade indifferenziata a quelle di testicolo. I primi elementi che possono essere attribuiti alla linea germinale maschile sono degli spermatociti I in profase (pachitene). Dovrei dedurre che gli stadi intermedi sono molto rari e che le divisioni spermatogoniali sono molto rapide, oppure che da uno stadio di elemento indifferente (protogonio o deutogonio) si passa al differenziamento sessuale con la comparsa di spermatociti.

I nidi formati dagli spermatociti hanno un contorno (in sezione) rotondo o leggermente ovale, raramente irregolare, dalle dimensioni di μ 23—26. Il limite tra i singoli nidi non è sempre bene demarcato. Gli stessi sono abbastanza ravvicinati gli uni agli altri, ma gli intervalli non sono mai superiori alla metà del diametro di un nido. Verso la periferia dell'organo i nidi sono ravvicinati in modo da tappezzare letteralmente la superficie interna della tunica propria. In una sezione di gonade si possono contare all'incirca un centinaio di nidi (dimensioni della sezione μ 410 × 161).

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Oltre agli elementi della linea germinale (le singole categorie dei quali verranno descritte più avanti), sono presenti nel testicolo delle particolari cellule di tipo indifferenziato, poste specialmente alla periferia dell'organo, immediatamente aderenti alla tunica propria, contigue alla cellule dello strato peritoneale (di cui si notano nettamente i nuclei), oppure dislocate qua e là nell'interno del viscere tra i nidi di elementi germinali, o anche compenetranti gli stessi.

Si tratta di cellule a contorno piuttosto regolarmente circolare, dalle dimensioni molto variabili, potendo andare da μ 3,75 a 7,5 (in media μ 5,7), caratterizzate dal materiale cromatinico costantemente in rimaneggiamento di tipo profase (raramente metafase), e dalla mancanza di limite nucleo-citoplasmatico (fig. 9 t, u, v, w, x). Il citoplasma è costantemente incoloro, il materiale cromatico è rappresentato da condensazioni molto grossolane, irregolari, a volte anulari, a volte ancora a forma di nodo più o meno irregolare, miste a della cromatina finissimamente polverizzata. Sono indotto a interpretare tali elementi, con qualche riserva, come cellule epiteliali (epitelio germinativo), omologhe forse alle cellule dell'epitelio ovarico di cui parla BAUER a proposito della *Tipula* (1933). Le chiamerei pertanto «cellule stromatiche» (a funzione interstiziale?). Credo pure di poter identificare tali elementi con quelli descritti a proposito di una gonade indifferenziata, dislocati alla periferia del viscere, e in cui si notavano, sebbene vagamente, dei limiti cellulari. In tale caso si concluderebbe che il carattere epiteliale di tali cellule è differenziato già in stadi molto precoci.

Il testicolo in condizioni definitive di sviluppo (larva nel periodo immediatamente precedente la ninfosi, ninfa e adulto) appare come un sacco in cui stanno senza ordine apparente i gruppi di spermatozoi densamente uniti tra loro e disposti tipicamente a vortice. Dimensioni medie μ 230 × 670 (fig. 8).

Si notano qua e là elementi indifferenziati che non so se attribuire a spermatogoni o a spermatociti I [1], inoltre diversi elementi identificabili con le cellule che io ho considerato con qualche riserva come stromatiche. Oltre a tali elementi cellulari la massa di spermi è circondata da granuli più o meno grossolani, tinti debolmente in grigiastro, a contorno più o meno rotondeggiante o irregolare, di dimensioni che raggiungono al massimo quelle di uno spermatide, potendo essere di molto inferiori. Non sono in grado di stabilire se si tratta di granuli di secreto (che concorrerebbe alla formazione del liquido seminale) oppure di prodotti di degenerazione di elementi sessuali (spermatidi, ad esempio), od ancora del risultato dell'eliminazione di citoplasma che si ha nella spermioistogenesi.

Un'altra particolarità presente costantemente nei testicoli maturi è una formazione cistica, rappresentata da un inviluppo granuloso più o meno trasparente, solo a volte molto oscuro, che contiene diversi inclusi di forma globosa o lievemente irregolare e di dimensioni molto variabili. Precisamente le dimensioni di tali cisti vanno da μ 7,5 × 9 a μ 19 × 22. Non posso precisare la natura di tali formazioni. Ritengo tuttavia trattarsi di produzioni degenerative (vedi quanto segue), risultanti forse dalla fusione di diversi elementi sessuali (spermatociti I ?) degenerati (vedi anche fig. 8).

Voglio descrivere a tale proposito una formazione molto notevole riscontrata in una sezione di testicolo. Si tratta di un gruppo di elementi cellulari di dimensioni notevoli (μ 7,8 × 9) disposti a rosetta molto regolarmente circolare, poco distante dalla parete del testicolo stesso, e del tutto isolata dalla massa degli spermatozoi circostanti.

I singoli elementi hanno contorno irregolare, spesso piriforme o ovale, citoplasma colorato coll'ematossilina ferrica in grigio scuro, nucleo ben distinto dal citoplasma e piccolo in confronto agli elementi sessuali normali, a contorno irregolare, colla cromatina densamente compatta in modo da comparire, specialmente a debole ingrandimento, nero (fig. 10 a, b, c, d). La natura degenerativa di tali elementi è chiarita dall'esame di un gruppo di elementi cellulari posti in un altro punto della sezione X : si notano tutti gli stadi di transizione da un aspetto uguale a quello dei normali spermatociti I (sebbene di dimensioni nettamente maggiori) fino alle forme su descritte, e si assiste alla progressiva condensazione del materiale cromatinico, che fa pensare ad una vera e propria picnosi. E' pertanto da considerare con certezza tutte queste cellule a nucleo compatto e scuro come prodotto di degenerazione di spermatociti I.

[1] Sarebbe difficile ammettere trattarsi di spermatogoni, elementi che rimangono molto spesso in testicoli maturi e che si trovano misti a gruppi di spermatozoi, dal momento che nel testicolo in via di sviluppo non riesco a vedere mai tali elementi, le più giovani cellule sicuramente differenziate essendo spermatociti I. Non ho tuttavia studiato abbastanza i preparati di testicolo maturo per poter affermare qualcosa di più sicuro sull'argomento.

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DESCRIZIONE DEGLI ELEMENTI GERMINALI.

Gli spermatociti I (o di I ordine) (fig. 9 e—k) sono cellule a contorno irregolare, a limite nucleo-citoplasmatico poco chiaro, in genere a citoplasma limitato a un sottile alone a volte perinucleare, a volte ancora disposto più da una parte del nucleo che dall'altra. In certi casi (nelle sezioni massime dei nidi) contorno delle cellule addirittura piriforme, ricordando i nidi di spermatogoni di altri Insetti in cui gli elementi germinali hanno peduncoli che possono confluire al centro a formare veri e propri sincizi. Nelle cellule piriformi il nucleo è spostato nella parte più larga della cellula, ricordando quindi la polarità di certi epiteli glandolari. Le dimensioni di questi elementi (che sono i più grandi di tutta la serie maschile) si aggirano dai μ 4,5 ai 7,5 in media μ 6,1), mentre il nucleo varia da μ 4,5 a 6,7 (in media μ 5,8). In certi casi le cellule hanno un netto contorno ovoide.

Quasi tutti gli spermatociti I sono in divisione, e si possono distinguere facilmente le varie modificazioni del materiale cromosomico. Caratteristica è la sincronicità dell'evoluzione dello stesso, per cui si notano nidi ad elementi in pachitene (molto frequenti), altri con segni di diplotene più o meno evidente, altri ancora in metafase o in anafase [1].

Lo stadio di pachitene (fig. 9 e) è rappresentato da un gomitolo di filamenti cromatinici relativamente tenui, a granulazioni molto fini disposte qua e là lungo il de decorso del filamento stesso. Non si ha alcun cenno di polarizzazione («bouquet») come si riscontra in molte specie animali e vegetali in tale stadio. In genere il gomitolo è diffuso molto omogeneamente in tutto il nucleo, senza particolari rapporti con la superficie interna della membrana nucleare. Il diplotene (non molto tipico) è indicato da un aspetto più spesso dei filamenti stessi, sui quali si notano delle granulazioni più grossolane di quelle che si hanno nel pachitene (fig. 9 f).

Numerosi elementi si trovano in stadi riferibili alla metafase e all'anafase (fig. 9 g—k). Il materiale cromosomico non è mai netto, nè è mai determinabile il numero dei cromosomi. Gli aspetti più tipici nei preparati da me esaminati sono quelli dell'inizio della anafase in cui si notano dei cromosomi ricurvi ad U (coi bracci di lunghezza diversa) che si allontanano dalla piastra equatoriale, mentre altri rimangono ancora nella condizione di metafase (più o meno accollati gli uni agli altri). Devo dedurre che tale stadio dura per un periodo relativamente lungo. Osservai pure qualche singola anafase col materiale cromosomico del tutto impacchettato.

Alla prima divisione maturativa seguirebbe una breve intercinesi (presenza di elementi interpretabili per le dimensioni minori, da μ 4 a 5,2, in media μ 4,5,

[1] Non sono riuscito a metter in evidenza nettamente lo stadio di diacinesi, forse a causa di una fissazione non troppo adeguata, oppure per la difficoltà di trovare elementi in tale stadio, questo durando forse per un periodo di tempo molto breve. Si vedrà nella discussione circa l'aspetto della diacinesi in altri Chironomidi, secondo i dati degli AA.

come spermatociti II col nucleo in condizione di riposo). Tuttavia la gran parte degli spermatociti di II ordine sono in divisione, essendo presenti tutti gli stadi della divisione: rimaneggiamento nucleare indice di inizio di profase, stadi più o meno netti di profase con un gomitolo cromosomico piuttosto irregolare e in cui i singoli filamenti non si possono seguire con un decorso molto lungo, metafase e anafase (fig. 9 l—o). Da notare che le figure cromosomiche nella metafase di tali elementi sono le più nitide di tutti gli stadi, e in qualche preparato (fig. 9 n) è stato possibile avvicinarsi alla determinazione del cariotipo: ho osservato particolarmente una piastra equatoriale in cui si notavano 9 elementi, di cui uno centrale sferico, gli altri più bastoncelliformi, 4 essendo ben separati, gli altri 4 invece ravvicinati ad un estremo.

Da notare che gli spermatociti II, come i I, formano nidi; i singoli componenti di un nido però non sono uniti gli uni agli altri e non assumono mai una forma ovoide o a pera, il contorno essendo anzi molto spesso regolarmente rotondeggiante.

Alla seconda divisione maturativa segue lo stadio di spermatide (fig. 9 p). Questi elementi sono caratterizzati dalle dimensioni inferiori a quelle di tutti gli altri elementi germinali, variando da μ 2,25 a μ 3,75 (in media μ 3,4). Sono disposti in gruppi che non si possono denominare più nidi, essendo bene staccati e distanziati gli uni dagli altri. Il contorno cellulare è leggermente irregolare, angoloso, o anche rotondo. Il nucleo, negli elementi che si possono denominare tipici spermatidi, presenta netti segni di differenziazione cromatinica, che devono essere interpretati come i resti della telofase II. Appena il nucleo è in riposo inizia la spermioistogenesi. Il volume cellulare si riduce, la forma si fa ovale, ellittica, indi sempre più allungata, mentre il nucleo subisce le solite alterazioni di tipo regressivo (fig. 9 g—s). (Non si possono scorgere maggiori dettagli, come il paranucleo o l'acrosoma, colla tecnica da me impiegata). Alla fine si giunge alle condizioni definitive di spermio maturo [1].

OVOGENESI.

CARATTERISTICHE GENERALI DELLA GONADE FEMMINILE.

L'ovario nel genere *Chironomus* (osservato e descritto sommariamente da vari AA.) appartiene alla categoria generale degli ovari dieroistici, in cui cioè non è possibile differenziare delle unità anatomiche inferiori (ovarioli), essendo invece costituito da un insieme di elementi germinali e di cellule di tipo epi-

[1] Lo spermatozoo in *Chironomus* appartiene alla categoria degli spermi flagellati tipici. Le dimensioni sono sui μ 9—11 (parte cromatica, rappresentata da un filamento nero, all'estremità acutamente filiforme), lo spermatozoo essendo però più lungo, distinguendosi vagamente una parte terminale quasi incolora. Nei preparati fissati e colorati lo spermio appare a decorso più o meno ondulato.

teliale che formano delle cisti indipendenti le une dalle altre, e diffuse irregolarmente in seno allo ovario stesso.

L'ovario è provvisto esternamente di due tuniche, l'esterna o peritoneale e l'interna o tunica propria. La prima è caratterizzata da nuclei molto allungati, a cromatina di tipo granuloso o polverizzato, senza evidenti limiti cellulari, applicati molto intimamente all'esterno della tunica propria. Quest'ultima è una membrana anista non sempre bene dimostrabile nei preparati colorati colla tecnica da me impiegata. Non sono riuscito a differenziare, internamente alla tunica propria, uno strato analogo all'epitelio ovarico di cui parla BAUER per la *Tipula* (strato che si ispessisce collo sviluppo dell'ovario, e provvisto spesso di cellule in mitosi): può darsi che tale strato sia presente soltanto negli stadi iniziali della gonade, e che negli esemplari da me esaminati (in cui si nota sempre un certo numero di cellule ovariche in vitellogenesi più o meno avanzata) esso sia già evoluto a costituire i «cistociti» (o cellule follicolari), le cellule epiteliali del calice ovarico e le cellule che costituiscono i peduncoli ovarici. Inoltre nella specie da me studiata mancherebbe il filamento terminale («Endfaden») descritto da BAUER (1923) in *Tipula oleracea*. Non credo che tale struttura sia omologabile al legamento (sospensorio) repertato da me nella gonade indifferenziata, dal momento che la prima è, secondo il citato A., una struttura tipicamente cellulare, essendo inoltre in rapporti di continuità morfologica coll'«Epithelwulst», struttura pure assente in *Chironomus*.

Non s'osservano, almeno nei preparati colorati coll'ematossilina ferrica o coll'ematossilina -eosina, cellule riferibili alla categoria delle interstiziali [1], nè ancora delle differenziazioni interpretabili come tessuto connettivo.

In stadi iniziali l'ovario è rappresentato da un sacco subcilindrico (lûngo quasi 4 volte la propria larghezza) in cui stanno ammassate più o meno irregolarmente delle cisti di cellule follicolari, in mezzo alle quali è spesso facilmente dimostrabile una cellula germinale (fig. 1). Tali cisti hanno dimensioni massime di 15—21 μ, contorno rotondeggiante o leggermante ovale; in una sezione massima (equatoriale) vi si possono contare circa 12—13 cellule follicolari disposte intorno ad una cellula germinale rotonda, di dimensioni variabili da μ 5,25 a μ 7,5 più spesso però sui μ 6 (auxocita).

In preparati di ovari più maturi (dimensioni della gonade circa μ 115 × 420) si ha spesso un assetto delle singole cisti in serie lineari disposte radialmente intorno al calice ovario [2] di già ben differenziato, dimodochè, in una sezione longitudinale, verso gli estremi del calice stesso le serie hanno una disposizione

[1] Si vedrà nella discussione quale significato sia da dare secondo me alle «Zwischenzellen» di BAUER (1923).

[2] Traduco con «calice ovarico» l'espressione di BAUER «Eikelch». Tale struttura, che è stata osservata da GRIMM in *Chironomus* e da BAUER in *Tipula*, si continuerebbe distalmente coll'ovidotto. Io però non sono riuscito ad osservare il tratto di unione tra ovaio e ovidotto, e pertanto non ho seguito i rapporti tra quest'ultimo e il calice stesso.

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a raggiera, mentre lungo il rimanente del calice hanno posizione ortogonale rispetto all'asse principale del viscere (fig. 2). Le serie lineari (dalle dimensioni medie di 21×50—60) sono unite a gruppi di oociti più o meno sferici (che ricordano l'assetto tipico dei blastomeri nella morula) e distribuiti specialmente ai due poli dell'ovario. Tali gruppi misurano da μ 17 a 26. Le dimensioni dei singoli oociti variano molto, dipendendo strettamente dal grado più o meno avanzato di vitellogenesi. Gli intervalli tra gli ammassi di oociti sembrano, almeno nelle sezioni colorate coll'ematossilina ferrica, vuoti, senza differenziazione di tessuto connettivo o di cellule interstiziali.

In uno stadio più avanzato nello sviluppo della gonade si ha la formazione di peduncoli [1] che connettono alcune tra le cisti più centrali al calice ovarico. Queste cisti, che sono le più grandi fra tutte quelle presenti nella sezione (dimensioni μ 22×35), sono costituite da un oocita (dimensioni medie μ 19×26) unito, nel segmento prossimale della ciste stessa, ad una cellula nutrice, il tutto essendo circondato da uno strato di cellule follicolari. Le cisti sono unite a mezzo di un peduncolo solido, costituito di cellule epiteliali strettamente unite le une alle altre, alla cavità del calice, o meglio alla sua parete epiteliale. L'aspetto complessivo delle cisti peduncolate attaccate al calice ovarico ricorda vagamente una spiga (fig. 3).

Oltre alle cisti peduncolate in tali ovari si notano numerosi gruppi di follicoli (cisti) sparsi più o meno irregolarmente, alcuni immediatamente vicini alle cisti peduncolate, altri del tutto indipendenti dalle stesse. Non ho mai osservato nelle sezioni esaminate peduncoli apicali («Apikalstiele» di BAUER 1923) confrontabili con quelli trovati da BAUER nell'ovario di *Tipula*, che unirebbero dei follicoli diversi nella regione periferica degli stessi, e precisamente follicoli più sviluppati. Io mi sono limitato ad osservare una specie di prolungamento a cono del rivestimento follicolare nel polo apicale, senza però delle connessioni con i follicoli viciniori. E' da notare per inciso che secondo BAUER in *Tipula* le cellule nutrici sono distali rispetto al calice ovarico, nel caso dei *Chironomus* invece prossimali.

In quanto al calice ovarico [2] è da dire solo che è costituito da una cavità centrale rivestita di cellule epiteliali e separato a mezzo di queste dagli elementi germinali. Credo di osservare degli ammassi irregolari di cellule di tipo epiteliale verso uno dei poli del calice stesso, ma non posso escludere trattarsi di sezione tangenziale alla superficie del calice stesso in cui si prendono molte cellule che costituiscono la parete del calice. In ovari più sviluppati (fig. 4) le cisti aumentano di volume, il peduncolo non è più visibile (e così pure le cellule nutrici), mentre le cellule follicolari (cistociti) si appiattiscono intorno all'ovo-

[1] Traduco con «peduncolo ovarico» l'espressione di BAUER «Eistiele». GRIMM non ha descritto tale caratteristica per l'ovario di *Chironomus* nei suoi lavori del 1870—71.

[2] Nei Culicidi (KULAGIN) si ha al posto di un calice un cordone centrale («Strang»). Anche LÉCAILLON (teste KULAGIN) parla di tale cordone centrale. A tale struttura sarebbero uniti i peduncoli ovarici.

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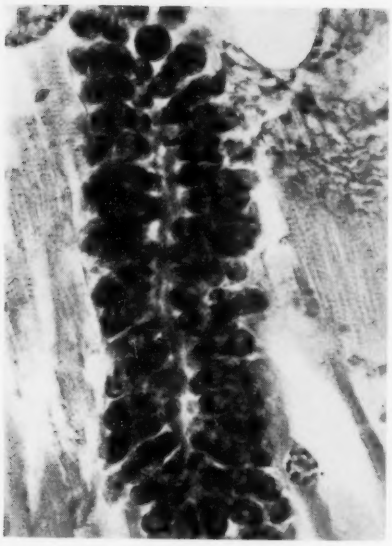

Fig. 2.

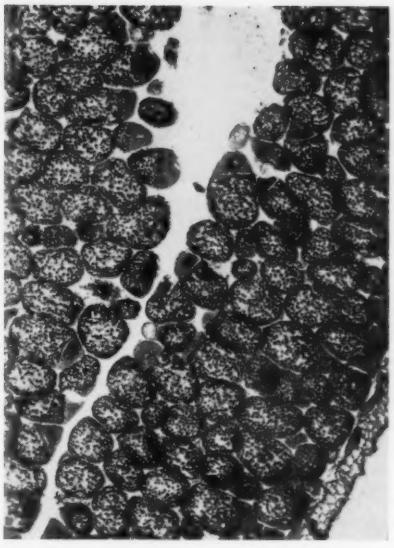

Fig. 4.

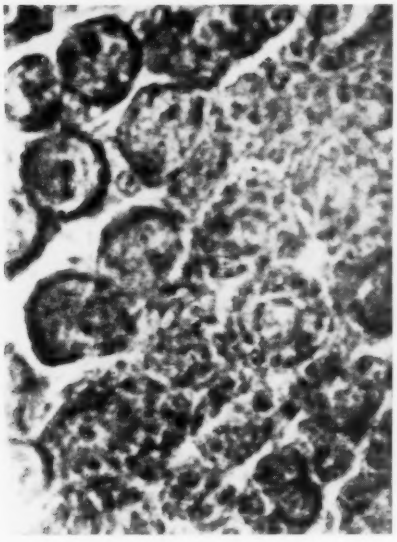

Fig. 1.

Fig. 3.

Fig. 1. Ovario molto giovane, con auxociti circondati da cellule follicolari; oociti I in accrescimento con tracce marcate di vitellogenesi. 1050 ×.

Fig. 2. Ovario in stadio successivo di sviluppo. Vi si distingue il calice ovarico, al centro, da cui si dipartono gruppi radiali di oociti. 240 ×.

Fig. 3. Stadio successivo di sviluppo; cisti ovariche con cellula nutrice, il tutto attaccato al calice ovarico a mezzo di peduncoli ovarici. 470 ×.

Fig. 4. Ovario in condizioni quasi mature; oociti ricchi di deutoplasma (granuli neri); ooplasma confinato in un angolo della cellula a mo' di cappuccio (vi si nota il materiale cromatinico piuttosto condensato e scuro). 75 ×.

(1) Tutte le figure, come pure le fotografie, sono state fatte da preparati fissati in Karpetschenko e colorati coll'Ematossilina ferrica. Le figure sono state delineate colla camera lucida, i particolari più fini essendo poi aggiunti a mano libera. Gli ingrandimenti sono i seguenti: fig. 10, s. oc. 4, ob. imm. 1/18″; tutte le altre, oc. 8, ob. imm. 1/18″.

cita che rivestono assumendo una netta forma lamellare. A tale stadio il calice è difficilmente dimostrabile; da notare pure che in tali ovari non si notano degli oogoni, presenti in genere in tutti gli stadi precedenti.

DESCRIZIONE DEGLI ELEMENTI GERMINALI. (1)

Gli elementi più giovani di cui si può seguire la seriazione sono gli oogoni (fig. 10 e—i). Questi non sono molto dissimili dai gonociti (protogoni e deutogoni) descritti a proposito della gonade indifferenziata. Le dimensioni medie si aggirano sui μ 3,6 per 5,2. Il contorno è più o meno rotondeggiante in alcuni, in altri nettamente ellittico. Si trovano specialmente alla periferia dell'organo, liberi o più spesso addossati a nidi di oociti, e in tale caso presentano spesso dei segni di compressione, assumendo forma allungata, non solo, ma pure ricurva, colla concavità del contorno in relazione al nido cui aderiscono. Dimensioni del nucleo leggermente inferiori a quelle cellulari. Sono spesso in mitosi. Si osserva abbastanza spesso lo stadio di profase, caratterizzato da un netto gomitolo di materiale cromatinico formato da filamenti abbastanza grossolani; a volte ancora il materiale cromatinico è condensato in zolle a volte anulari a volte irregolari e polarizzate in un angolo del nucleo. Osservai qualche metafase presa di lato e una figura non troppo netta di anafase.

Oociti (fig. 10 l—u). I primi oociti (auxociti) si possono considerare elementi cellulari in cui si può scorgere a mala pena un sottilissimo alone di ooplasma colorato coll'ematissilina ferrica più fortemente di quello degli oogoni (e deutogoni), a contorno piuttosto rotondeggiante, e provvisto di un rivestimento di cellule follicolari (epiteliali). In un preparato le cellule follicolari rivestono completamente la cellula germinale, in cui il contorno è perfettamente rotondo, le dimensioni vanno da μ 5,25 a 7,5 (in media μ 6) e il nucleo è in condizioni di perfetto riposo. In altri preparati (fig. 10 t e u) le cellule follicolari sono addossate, in numero di 1—2 e più, molto intimamente alla cellula germinale, tanto che a volte non si osserva un netto limite cellulare tra i due tipi di elementi (2). Il citoplasma presenta già tracce di vitellogenesi (colorito più scuro di quello degli oogoni). Coll'aumento della vitellogenesi aumentano le dimensioni cellulari degli oociti e si notano delle figure nucleari che indicano l'inizio della meiosi.

Parecchi elementi presentano nel nucleo un gomitolo più o meno tenue, non sempre ben discernibile per lunghi tratti, di materiale cromatinico (fig. 10 l).

(1) Vi sono comprese le cellule nutrici. Le cellule epiteliali, pur non essendo da considerare nemmeno geneticamente affini alle cellule germinali, saranno descritte alla fine di questo capitolo.

(2) Non so se si può parlare di un vero e proprio sincizio. GIARDINA ammette (pag. 467) che negli Insetti le cellule epiteliali abbiano rapporti di contiguità, mai di continuità, cogli oociti. Credo sia inutile osservare che tali concetti sono sempre molto difficilmente dimostrabili in pratica, dipendendo molto dai mezzi che abbiamo a nostra disposizione (sia materiale che tecnica), per metter in evidenza tali particolarità strutturali.

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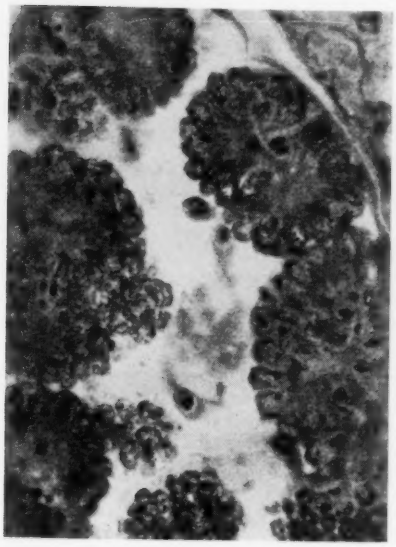

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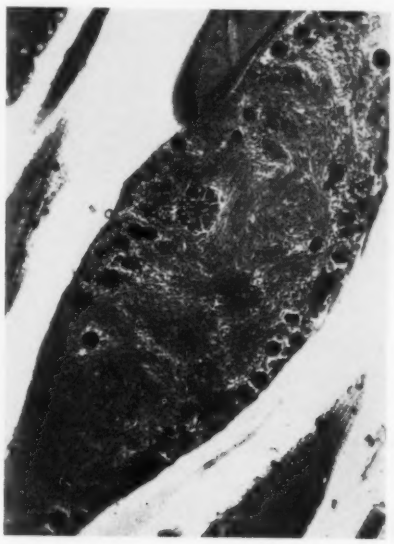

Fig. 8.

Fig. 5.

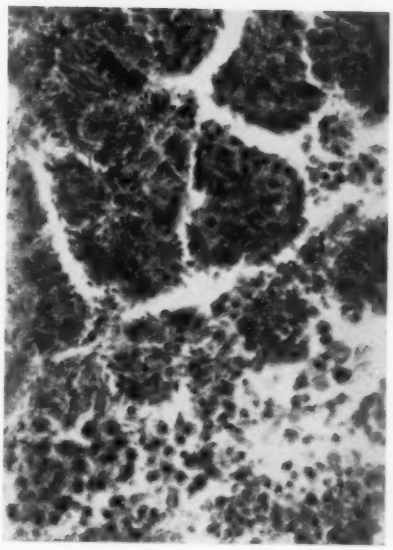

Fig. 7.

Fig. 5. Oocita col nucleo in cui si distinguono le «zolle di cromatina» e il citoplasma molto scuro per lo stadio avanzato di vitellogenesi. 840 ×.

Fig. 6. Testicolo giovane, con gruppi di spermatociti I in pachitene, disposti a rosetta; nel nido di destra si nota cellula di tipo stromatico (nucleo molto scuro, irregolare). 760 ×.

Fig. 7. Testicolo in stadio successivo di sviluppo; diversi stadi di spermatogenesi (spermatociti I e II, spermatidi) e inizio della spermioistogenesi. 460 ×.

Fig. 8. Testicolo maturo con gruppi di spermatozoi disposti a vortice; cisti non meglio interpretate (alla periferia); si nota a destra, verso il margine, una rosetta di elementi in via di degenerazione. 170 ×.

Le dimensioni vanno da quelle degli oogoni fino a un masmo di μ 7,5 × 10. Considero che tale stadio rappresenti il leptotene. I filamenti non sono polarizzati e non presentano l'aspetto di «bouquet». Lungo le briglie cromosomiche sono ben distinti i cromomeri, posti piuttosto uniformemente lungo il decorso degli stessi. Non si nota un cromocentro.

In qualche singolo elemento (μ 8 × 10) si nota un netto aspetto di pachitene: il gomitolo cromosomico è rappresentato da filamenti molto spessi ben visibili lungo il loro decorso (fig. 10 m), a cromomeri che formano delle vere e proprie bande, che ricordano vagamente quelle dei cromosomi giganti.

Non sono mai osservabili degli stadi di diplotene o di diacinesi, repertati in altri gruppi di Insetti nell'ovogenesi. Un aspetto molto caratteristico del materiale nucleare è la formazione di «zolle di cromatina», caratterizzato da ammassi scuri a contorno irregolare di cui, alcuni bene staccati tra di loro, altri ancora molto vagamente separati, notandosi tra di essi in piani diversi delle fini briglie di unione (fig. 10 n). Il numero di tali zolle è male determinabile: in alcune sezione si può calcolare uguale a 5. Le cellule il cui nucleo presenta tale caratteristica sono degli oociti in stadio abbastanza avanzato di vitellogenesi (μ 9 × 16) in cui il limite nucleocitoplasmatico è ben visibile, ed il citoplasma ridotto ad un anello più sviluppato a un lato o ai due poli della cellula (ved endu fig. 5).

Si notano ancora degli elementi in stadio di vitellogenesi più avanzata (dimensioni medie 14 μ) col materiale cromatinico suddiviso in blocchetti o in masserelle spesso subrettangolari, angolose (fig. 10 f), a volte ancora in una massa di granuli più o meno grossolani, in certi esemplari del tutto omogeneamente diffusi in seno al nucleo, in altri ancora disposti in modo da costituire come una traccia di gomitolo (stadio posteriore al pachitene?) (fig. 10 g). In altri elementi ancora (dimensioni uguali a quelle degli elementi ora descritti) si notano delle zolle di cromatina che presentano un frazionamento in zolle secondarie o un assetto ad anelli più o meno irregolari (fig. 10 o). Non so se tali formazioni seguano direttamente a quelle a tipiche zolle descritte poco sopra. In oociti di dimensioni maggiori il nucleo ha sempre più i segni di riposo, la cromatina assumendo negli ultimi stadi un aspetto finissimamente polverizzato, potendosi scorgere solo difficilmente delle maglie delicate qua e là in seno al carioplasma.

Le massime dimensioni osservate negli oociti in cui non era ancora comparsa la formazione di tuorlo vero e proprio (deutoplasma) sono quelle di μ 42 × 60.

Fig. 9 a—d. gonociti: a. in riposo; b. profase; c. metafase; d. cellula in cui è ben evidente la distinzione tra citoplasma e nucleo. — e—k. spermatociti I: e. pachitene; f. diplotene iniziale; g. aspetto molto frequente ad osservarsi e attribuibile a inizio di metafase; h. tipica metafase; i. e j. inizio della separazione dei cromosomi nell'anafase; k. tipica anafase. — l—o. spermatociti II: l. in riposo; m. profase; n. metafase; o. anafase. — p. spermatide. — q—s. tre stadi successivi della spermioistogenesi. — t—x. vari tipi di cellule indifferenziate di, tipo stromatico: aspetto di nucleo a materiale cromatinico polverizzato, nucleo in profase e in metafase (figure poco tipiche).

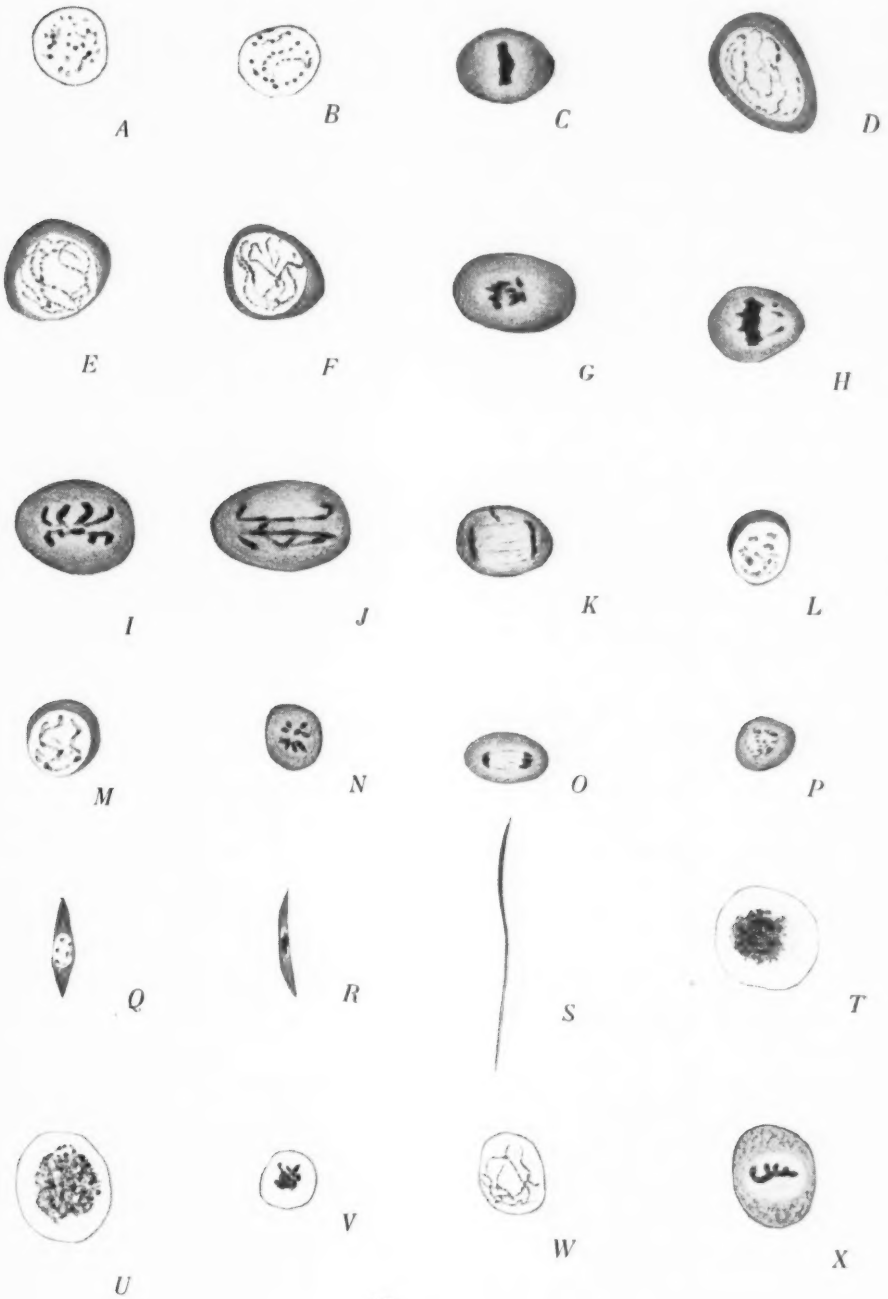

Fig. 9.

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Degli oociti (come è stato già detto a proposito della struttura anotomo-microscopica dell'ovario) sono accompagnati da una cellula nutrice (fig. 3 e 10 r). Le dimensioni di tali oociti sono piuttosto costanti, e si aggirano sui μ 19 × 26.

Allorchè gli elementi hanno raggiunto tali dimensioni (in genere) inizia la formazione del deutoplasma, per cui la cellula assume un aspetto molto tipico, essendo come suddivisa in due parti, una rappresentando il citoplasma e il nucleo, l'altra il deutoplasma (fig. 4). A volte in preparati di sezioni fissate in Karpetschenko e colorate colla ematossilina ferrica spicca un netto spazio vuoto tra il primo e il secondo. Le minime dimensioni osservate in esemplari provvisti di deutoplasma erano di μ 67 × 98, aumentando indi progressivamente fino alla completa maturità dell'uovo [1]. In un preparato di ovario molto maturo le dimensioni massime erano μ 110 × 172. In questi elementi il nucleo è confinato in un angolo della cellula, il materiale cromatinico essendo rappresentato da granuli scuri, molto irregolarmente e densamente ammassati, oppure anche essendo polverizzato e più o meno rarefatto. Il citoplasma ha conservato il carattere tintoriale che aveva negli oociti in accrescimento; solamente verso il deutoplasma i margini sono poco netti, notandosi come una compenetrazione del primo nel secondo. Nel deutoplasma si notano essenzialmente granuli di varie dimensioni, da appena percettibili fino a 10 μ, tinti fortemente in nero coll'ematossilina ferrica. Tra i singoli granuli rimangono degli spazi vuoti molto cospicui (dovuti all'asportazione dei lipidi?) (ved fig. 4).

Si è già accennato varie volte alle cellule nutrici. Queste sono degli elementi indifferenziati, a contorno rotondo più spesso ovale-ellittico coll'asse maggiore ortogonale a quello della ciste ovarica (che è poi lo stesso del peduncolo), a volte leggermente angoloso evidentemente da compressione degli elementi viciniori (oocita distalmente al calice ovarico, strato di cellule follicolari in relazione alla parete della cisti con cui la cellula nutrice contrae rapporti molto intimi). Le dimensioni della cellula si aggirano sui μ 8,5 ca. Il citoplasma è perfattamente omogeneo (in preparati fissati in Karpetschenko e colorati coll'ematossilina ferrica) tinti uniformemente di grigio piuttosto chiaro, col

[1] In alcuni preparati negli oociti ricchi di deutoplasma il citoplasma (aderente al nucleo) è ridotto ad una sorta di cappuccio (o calotta) molto caratteristico che riveste da un lato il deutoplasma stesso.

Fig. 10 a—d. stadi successivi di degenerazione di elementi maschili spermatociti I); notare nella cellula d. il tipico aspetto picnotico del nucleo. — e—i, oogoni: e. in riposo; f. inizio di rimaneggiamento del materiale cromatinico; g. profase; h. metafase; i. anafase. — l—q. oociti I in vari stadi di sviluppo: l. leptotene (verosimilmente); m. pachitene; n. presenza delle tipiche «zolle di cromatina»; o—q. oociti col materiale cromatinico in progressivo frazionamento, come segno di passaggio a condizioni di riposo; notare il contemporaneo aumento delle dimensioni cellulari. — r. cisti ovarica (*c*) con oocita (*o*) e cellule nutrici (*n*), attaccata alla parete del calice ovarico (*c ov*) a mezzo del peduncolo ovarico (*p ov*). — s. cellula nutrice. — t. e u. oociti (auxociti) con una, rispettivamente due, cellule follicolari. — v—y. cellule epiteliali di diverso tipo, sede e funzione: v. e w. cellule di aspetto lamellare rivestenti degli oociti maturi (la prima vista dal di sopra, la seconda io sezione trasversale).

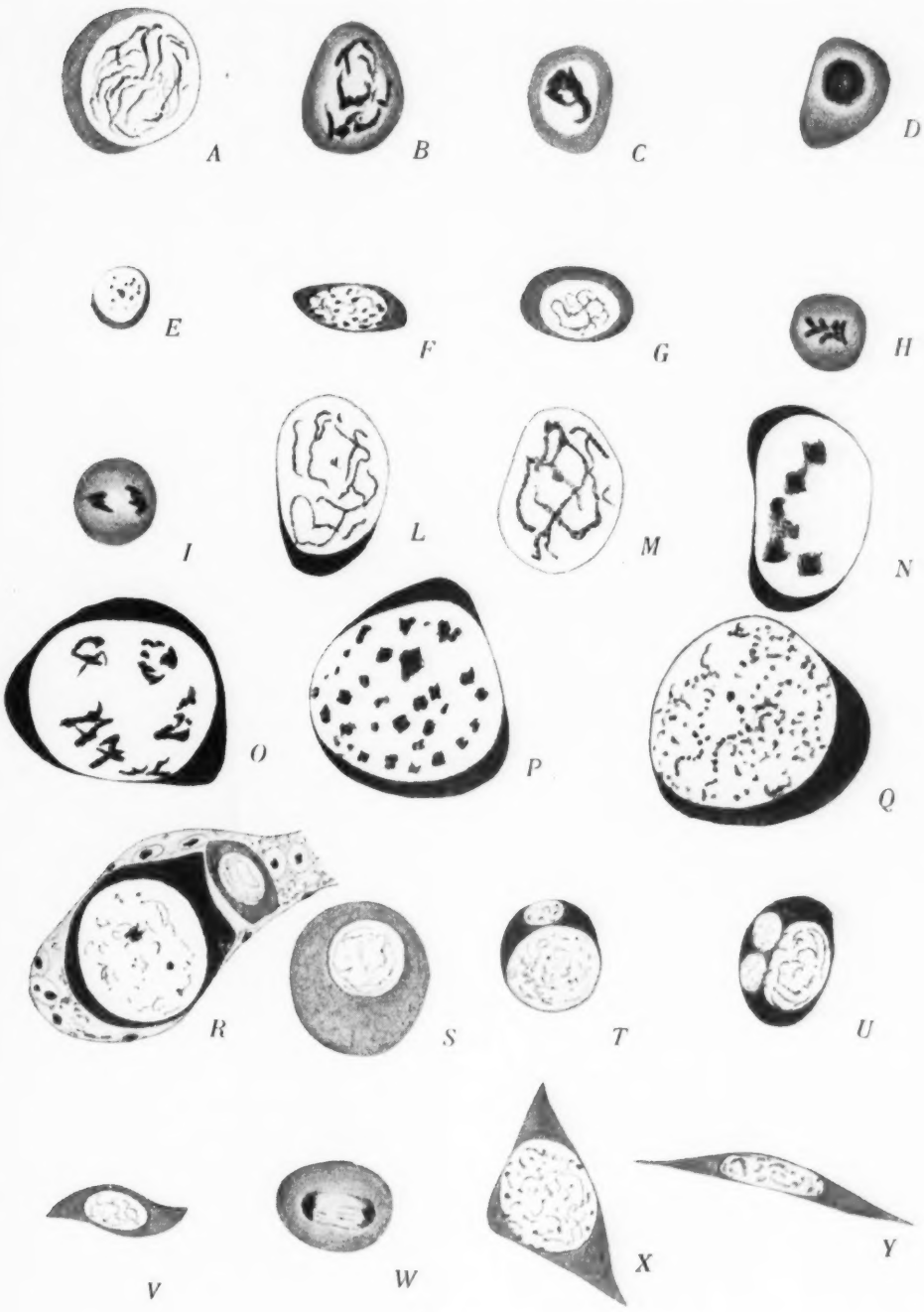

Fig. 10.

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limite nucleo-citoplasmatico molto ben evidente (fig. 10 r e s). Nucleo centrale, cromatina rappresentata da un reticolo delicatissimo su cui si scorge qua e là qualche granulo finissimo e distribuito omogeneamente (fig. 10 s). Non vi sono condensazioni alla parete interna della membrana nucleare, nè all'interno del nucleo stesso. Non vi sono tracce di attività riproduttiva nè di fatti degenerativi. Mai si nota tra cellula nutrice e cellula uovo una contiguità tale che faccia pensare ad una partecipazione diretta da parte della prima al trofismo della seconda.

Io sono riuscito a scorgere tali elementi solamente in determinate sezioni di ovario, e solo in relazione ad oociti di dimensioni medie di μ 19 × 26. Non ho potuto seguire l'evoluzione di entrambi onde stabilire se la cellula nutrice concorre efficacemente alla nutrizione della cellula uovo o meno. In tutti i casi le dimensioni piuttosto piccole del nucleo ed il suo contorno perfettamente regolare fanno pensare che tale cellula non sia deputata ad una attività molto intensa nel senso del trofismo cellulare.

Le cellule epiteliali sono elementi polimorfi (fig. 10 v—y), a funzione evidentemente protettiva o meccanica, e che sono deputati a formare da una parte il rivestimento degli oociti (formando così le «cisti ovariche») e dall'altra la parete del calice ovarico nonchè i peduncoli ovarici (limitatamente a determinati stadi di sviluppo della gonade). In relazione alla diversa sede e funzione le cellule che io denomino epiteliali a causa del loro aspetto anatomo-microscopico, senza voler inferire minimamente sul loro significato genetico, e che ritengo appartenere tutte ad un'unica categoria cellulare (a origine comune), si hanno delle modificazioni strutturali notevolissime.

In genere nei primi periodi di sviluppo le cellule epiteliali formano un rivestimento più o meno omogeneo intorno alle cellule sessuali (auxociti). In genere i contorni cellulari sono assai poco distinti (colla colorazione da me usata), potendosi differenziare nettamente solo il nucleo (le cui dimensioni vanno da μ 2,25 a μ 3,25). Il nucleo è bene separato dal resto della cellula, circondato da un alone quasi incoloro, e rappresentato da una masserella centrale di materiale cromatinico scuro, a contorno irregolare e dalle dimensioni oli μ 1,8 circa. Si direbbe dall'aspetto trattarsi di nucleo in profase. Un'osservazione più attenta del materiale nucleare rivela una struttura finissimamente polverizzata, tra cui spiccano delle zollette più grossolane, scurissime, del tutto irregolari. Le cellule epiteliali conservano a un dipresso tale struttura anche nella formazione dell'epitelio del calice ovarico (che ha un carattere di epitelio cubico) dove a volte si riescono a differenziare i limiti cellulari.

Si è già accennato a proposito degli auxociti all'aspetto sinciziale del complesso formato dall'auxocita e dalle cellule follicolari (1 o 2 o poche). Tali condizioni sono però molto rare a riscontrarsi [1].

[1] Gross dice che le cellule follicolari delle camere (cisti) più giovani di un ovariolo di *Tipula* sono riunite in sincizio, non osservandosi i limiti cellulari. Non so se tale condizione è omologabile a quella riscontrata da me.

Osservo solo per inciso che non sono mai dimostrabili delle forme di transizione dagli elementi germinali (ad esempio oogoni) a elementi di carattere epiteliale.

Un aspetto particolare assumono le cellule epiteliali che costituiscono i peduncoli ovarici: il limite tra cellula e cellula è appena discernibile, le dimensioni sono ridotte e vi sono netti segni di compressione dovuti all'addensamento molto stretto degli elementi stessi. Tra cistocisti da una parte e epitelio del calice ovarico dall'altra, nonchè cellule del peduncolo, vi sono tutte le forme di transizione. A volte le cellule dell'epitelio del calice assumono un aspetto quasi lamellare, aumentando le loro dimensioni solo lungo due assi. Così ad esempio alcune cellule di tipo lamellare in mitosi (piastra equatoriale) raggiungono le dimensioni di μ 6,75 × 12. Non ho mai osservato cellule epiteliali in degenerazione nè in divisione amitotica, come è conosciuto per altri Insetti.

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Una differenziazione degna di nota abbiamo negli ovari maturi allorchè i cistociti (probabilmente in seguito all'azione di stiramento esercitata dall-oocita in accrescimento) assumono una forma nettamente lamellare (fig. 10 x e y). Sezioni trasversali di tali lamelle misurano ad esempio μ 2,4 × μ 23. Il diametro di un'altra cellula vista in sezione trasversa è μ 7,5 rispettivamente 13,5 circa, di cui il nucleo occupa μ 6,75. In certe cisti la dilatazione dei cistociti nel senso bidimensionale è tanto notevole che non si riesce quasi a veder traccia di elementi follicolari.

Abbiamo accennato a delle mitosi nelle cellule epiteliali; pur la regola essendo l'aspetto di profase descritto a proposito delle cisti di ovari giovani, si hanno spesso mitosi di cui si scorgono particolarmente gli stadi di metafase e anafase. Il materiale cromosomico è strettamente impacchettato per cui è impossibile contare il numero dei cromosomi (fig. 10 w). Non posso precisare a quale età o in quale formazione epiteliale le mitosi siano più frequenti, ma credo di osservare in genere più abbondantemente mitosi in ovari in medio sviluppo e nei cistociti più che nelle cellule dell'epitelio calicino.

DISCUSSIONE.

SPERMATOGENESI.

Per quello che riguarda la struttura della gonade maschile si è detto che il testicolo nella specie da me presa in considerazione è di tipo uniloculare o unifollicolare, cioè a dire del tipo strutturalmente più semplice. Anche per quello che riguarda la distribuzione degli elementi germinali nell'interno della gonade si hanno delle condizioni estremamente semplici: mancano la suddivisione in germarium, zona di accrescimento, zona di maturazione e zona di trasformazione presenti in molti gruppi di Insetti e che conferiscono un aspetto zonale ai follicoli testicolari. Mancano pure tipiche cellule nutrici. Nel nostro caso invece gli

elementi germinali costituiscono dei nidi a rosetta i quali, a differenza delle spermiocisti conosciute per molte specie di Insetti, non possiedono alcun involucro esterno di cellule follicolari. I nidi, con un relativo sincronismo da parte di tutti i propri elementi, passano attraverso gli stadi della maturazione (I e II divisione) e si trasformano in ammassi di spermi maturi. Questi alla loro volta non costituiscono degli spermiozeugmi, ma si trovano liberi nel testicolo, formando solo dei vortici che originano dalla stessa disposizione dei nidi di spermatociti [1].

Per quello che riguarda la spermatogenesi è da notare che nella specie da me studiata la gonade rimane indifferenziata a lungo, e i primi elementi sicuramente maschili a comparire sono gli spermatociti di I ordine. Seguirebbe che gli elementi indifferenziati sono rappresentati da protogoni e da deutogoni, usando la terminologia di GALGANO (1936). In questo senso dai deutogoni si originerebbero gli spermatociti I nel testicolo, mentre per l'ovario le condizioni sarebbero diverse in quanto elementi di tipo indifferenziato si trovano ancora nella gonade già differenziata in senso femminile, e pertanto si devono denominare oogoni.

In altri gruppi di Insetti (anche di Ditteri Nematoceri) si hanno invece gli stadi di spermatogonio [2] primario e secondario (da alcuni AA. non differenziati, e chiamati pertanto semplicemente spermatogoni). Da notare che spesso gli spermatogoni formano delle cisti in cui gli elementi sono riuniti a mezzo di peduncoli uniti in un centro citoplasmatico comune (*Notonecta*, POISSON, e *Syromastes*, GROSS). Tali nidi corrispondono evidentemente a quelli formati dagli spermatociti I riscontrati da me. Nel nostro caso non si tratta tuttavia di peduncoli e ancor meno vi è un'unione citoplasmatica centrale. Per quello che riguarda gli spermatociti è da osservare intanto che in diverse specie di Insetti (*Asilus notatus*, METZ, *Bombyx mori*, KAWAGUCHI) tali elementi all'inizio della profase sono molto piccoli, in qualche specie più piccoli degli spermatogoni, in altre più piccoli che in qualsiasi altro stadio. Io credo che in *Chironomus* quando l'elemento è già differenziato come spermatocita le dimensioni sono molto notevoli, piuttosto maggiori di quelle degli altri elementi.

In quanto al processo della meiosi, problema studiato in svariati Ditteri, anche Nematoceri, da molti AA., il primo lavoro, per quello che mi consta, fatto sui Chironomidi è quallo di WOLFF (1941). L'A. stabilisce che la meiosi in *Chi-*

[1] Interessante notare come nei *Culex*, cosi vicini sistematicamente ai *Chironomus*, secondo STEVENS (1910) si ha una struttura a cisti, le quali presentano un grado di maturità diverso a seconda che da un estremo della gonade si va all'estremo opposto. Si hanno tipicamente tutti gli stadi di spermatogenesi dallo spermatogonio allo spermatozoo. La maturazione inoltre, avverrebbe principalmente, se non totalmente, nella ninfosi. E anche in ciò *Culex* differirebbe da *Chironomus* in cui la maturazione è in genere precedente alla ninfosi.

[2] WOLFF trova spermatogoni in *Glyptotendipes* e non in *Chironomus*. METZ (1927) trovò in giovani larve di *Drosophila* spermatogoni, e in larve più avanzate nello sviluppo spermatogoni misti a spermatociti.

ronomus plumosus e *Glyptotendipes* è di tipo normale [1], la diacinesi essendo rappresentata da vere e proprie tetradi, sebbene molto semplici. (A proposito di *Chironomus* dice: «Am häufigsten sind die grossen Chromosomen mit zwei, nicht viel weniger zahlreich aber solche mit nur einem Chiasma», e a proposito di *Glyptotendipes*: «das Diplotän führt im weiteren Verlauf zu einer Abstossung beider Partner in allen nicht durch Chiasmata verbundenen Teilen und zu einer weiteren Kondensation. Die Chiasma-Orte treten erst in der Diakinese eindeutig hervor ... Es sind meist ein, seltener zwei Chiasmata pro Tetrade zu beobachten».) Come ho detto nella descrizione della spermatogenesi, io non sono riuscito colla tecnica da me impiegata, a metter in evidenza delle tetradi. Del resto gli aspetti del pachitene, del diplotene, della metafase e dell'anafase corrispondono con quelli raffigurati e descritti da WOLFF per i Chironomidi da lui studiati. E' da notare a tale proposito come anche in specie sistematicamente così vicine come *Chironomus* e *Glyptotendipes* vi sono delle modalità diverse nella meiosi; così ad esempio il pachitene nel primo è di tipo «bouquet», nella seconda no. Nella specie di *Chironomus* da me studiata non ci sarebbe nemmeno un aspetto a bouquet in tale stadio. Del diplotene io ho visto solo degli aspetti iniziali («früh Diplotän», come è indicato dal WOLFF). Le metafasi e soprattuto le anafasi hanno nei miei preparati aspetti molto simili a quelli raffigurati dall'A. citato per *Tendipes plumosus*. Anche in *Tendipes plumosus* naturalmente, come in tutti i Nematoceri studiati da WOLFF, mancano gli stadi di leptotene e di zigotene [2].

In quanto al cariotipo osservo che anche nel *Chironomus thummi* come nelle specie studiate da WOLFF la metafase II è quella che si presta meglio per lo studio dello stesso, i cromosomi essendo bene separati gli uni dagli altri e nettamente differenziati [3].

OVOGENESI.

Il primo punto in merito alla struttura dell'ovario che vuol essere discusso è la questione degli ovari dieroistici. L'ovario di *Chironomus*, secondo gli AA.,

[1] Presentano meiosi atipiche invece i Brachiceri e i rappresentanti della famiglia *Sciaridae* studiati da METZ. STEVENS che nel 1907 ha studiato la meiosi di varie specie di Brachiceri osserva che nelle specie esaminate non c'è nè aspetto di tetradi nè sinizesi nè bouquet nè spirema. In ciò si avrebbero, seccondo tale A., condizioni simili a quelle di Sagitta (STEVENS 1903 e 1905) e di certi Afidi (STEVENS 1905 e 1906).

[2] Anche METZ in *Drosophila* (1927) trova assenza di lepto- e zigotene. Da notare che in *Drosophila* anche gli stadi iniziali di diplotene sarebbero assenti. DOBZHANSKY tuttavia (1934) avrebbe trovato stadi di lepto- e diplotene, sebbene molto raramente, in spermatogenesi di *Drosophila*.

[3] Ho già detto che io considero il numero diploide di *C. thummi* maggiore di 8. Io ho contato in una piastra 9 cromosomi, dei quali uno nettamente più piccolo, rotondeggiante, tanto da poter essere considerato un eterocromosoma. Se il numero fosse veramente 9 e tale cromosoma fosse un eterocromosoma, si potrebbe assegnare alla specie da me studiata la formula 8 + X O (oppure 8 + X Y). Tuttavia, la tecnica usata non essendo la più adatta, non posso stabilire con sufficiente certezza quale sia il cariotipo di *C. thummi*; solo in linea provvisoria ritengo il numero diploide della specie uguale a 10 (anche per le considerazioni che si faranno più tardi a proposito del numero della zolle di cromatina degli oociti di tale specie).

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e secondo la terminologia morfologica usuale, apparterrebbe al tipo di ovario atipico e precisamente, nel senso di EIDMANN, dieroistico in quanto costituito non già da ovarioli veri e propri, ma bensì da un ammasso di singole cellule ovariche (circondate da cellule follicolari e provviste di cellule nutrici) senza alcun apparente legame le une con le altre, o al massimo disposte a catenella («Eikette» degli AA. tedeschi).

BERLESE ammette come base dell'architettura degli ovari gli ovarioli, e gli ovari dieroistici in questo senso sono, «quegli ovari in cui le pareti degli ovarioli mancano e i singoli follicoli sono contenuti liberamente nella parete dell'ovario che ha un aspetto di sacco nel quale sono alla rinfusa contenuti i follicoli a vario grado di sviluppo». Tuttavia tale distinzione di ovari dieroistici e ovari meroistici (o a ovarioli) non è sempre molto facile a mettersi in evidenza; ad esempio secondo GROSS (1903) l'ovario della *Tipula oleracea* appartienne al tipo degli «ovaria racemosa» («traubenförmigen Ovarien»), essendo costituito secondo tale A. da un calice ovarico a forma di lungo sacculo oppure di corto sacco, rivestito alla sua superficie di numerosi ovarioli. Secondo BAUER, che si è occupato della struttura dell'ovario della *Tipula paludosa,* non è esatto parlare di ovarioli ma bensì di «Eikette» essendo l'ovario di tale specie costituito sullo schema degli ovari dieroistici, come in *Chironomus* e in *Psychoda.* Tali «Eikette» sarebbero costituite da una serie di cisti ovariche gli elementi follicolari delle quali formerebbero uno strato continuo dall'una all'altra, senza però alcuna tunica comune alle diverse cisti, come dovrebbe essere il caso per i veri ovarioli.

KULAGIN descrive molto nitidamente l'ovario di *Culex* e di *Anopheles* e parla di una membrana (corrispondente secondo lo stesso A. alla «membrana propria» degli ovarioli di altri Insetti) che riveste i singoli ovarioli. Tale membrana però è visibile particolarmente in preparati *in toto* e specialmente in soluzione fisiologica. Essa sarebbe una produzione della tunica peritoneale che si addentra nel «sacco ovarico» (o ovario vero e proprio). Che tale membrana che riveste i singoli ovarioli (che del resto intanto sono tali in quanto possiedono la membrana stessa) sia molto difficile a mettersi in evidenza, sarebbe provato dal fatto che LÉCAILLON (a detta dello stesso KULAGIN) non l'ha descritta nel suo studio sull'ovario di *Culex.* Si vede pertanto che la distinzione di ovari dieroistici e meroistici dipende da particolarità strutturali molto fini e non sempre facilmente rilevabili, e precisamente sulla presenza o meno di una tunica propria (o membrana propria) che avvolge un dato numero di cisti ovariche disposte a catenella o disposte comunque. Si conclude automaticamente che anche in *Chironomus* esiste la possibilità che gli AA. sinora non abbiano osservata una si fatta tunica [1] e che la classificazione dell'ovario di *Chironomus*

[1] Bisogna notare tuttavia che qualche A. ha parlato di ovarioli a proposito di *Chironomus.*
GRIMM (1870—71) precisamente, descrive il tipico assetto di «Eikette» come un ovariolo («Eirohr»). Sembrerebbe effettivamente dalla descrizione che ne fa che egli abbia visto

come un ovario dieroistico sia soggetta a revisione. Personalmente, io ho esaminato soltanto preparati fissati e colorati (ematossilina ferrica e ematossilina-eosina) e con tale tecnica non sono riuscito ad osservare alcuna struttura di ovariolo, e pertanto mantengo per il momento la posizione acquisita dagli AA. già da molto tempo, che cioè l'ovario di *Chironomus* è di tipo dieroistico. Questo per quanto riguarda la struttura anatomo-microscopica del viscere.

In quanto ai suoi componenti cellulari, ho accennato nella descrizione a cellule germinali (oogoni e oociti), a cellule nutrici e a cellule epiteliali. Si noti sin d'ora la discussione che c'è stata e c'è praticamente tuttora in merito all'origine di tali tre tipi di cellule [1].

I primi AA., come KORSCHELT, JAWOROWSKY, ecc. ammettevano un'origine comune per cellule sessuali, cellule nutrici e cellule a funzione epiteliale. Dopo le osservazioni di HEYMONS 1891 [2], essenzialmente, gli AA. si sono orientati verso una duplice origine, da una parte degli elementi sessuali e cellule nutrici, dall'altra delle cellule epiteliali, i primi appartenendo alla linea germinale, i secondi invece provenendo dal mesoderma (somiti del periodo embrionale) e pertanto essendo di natura somatica [3]. GIARDINA studia nel 1901 l'origine delle cellule nutrici nel *Dytiscus* e viene alla conclusione che tanto gli oociti che le cellule nutrici provengano dalla stessa cellula germinale primitiva (oogonio). In quanto alle cellule follicolari, GIARDINA, pur appoggiando anche con le sue ricerche particolari sul *Dytiscus* l'idea che le due categorie di cellule abbiano

una membrana propria anista che circonderebbe le singole file di oociti («diese Eierstocksröhren bestehen... aus einer höchst elastischen stucturlosen Membran, die von innen mit einer Schicht Epithelialzellen ausgekleidet ist»). Lo strano è che non disegna tale membrana, anzi in relatà disegna (fig. 25 del lavoro del 1871) un complesso di cisti ovariche di tipo «Eikette» (nel senso di BAUER) simili ad aspetti osservati da me in *Chironomus thummi* e che non hanno in sè niente a che vedere coi veri ovarioli. Del resto nella stessa tavola disegna un ovariolo di *Musca domestica* in cui distingue, a differenza del *Chironomus*, un «Eierstockshülle», interpretabile certamente come una membrana propria.

IMMS (1934) nel suo trattato di Entomologia generale, parlando di *Chironomus*, riporta il seguente passo di MIALL e HAMMOND: «The morphology of ovaries is peculiar: each consits of a central axis radiating out from which is a large number of short ovarioles, the whole being enclosed in a delicate manner».

La LOMBARDI, tuttavia, studiando un'altra specie di Chironomide, *Cricotypus sylvestris*, dice che gli ovari sono «dieroistici, ad elementi (follicoli) formanti piccoli ragguppamenti disposti regolarmente intorno ad un asse centrale».

[1] Una rassegna critica di quanto è stato fatto e detto su tale punto si ha nel lavoro fondamentale di GIARDINA del 1901.

[2] I dati di tale A. trovano riscontro ancora in un lavoro di METSCHNIKOFF (1866).

[3] Degli AA. precedenti a GIARDINA voglio citare solo GRIMM dal momento che tale A. si è occupato esplicitamente del genere *Chironomus*. Mentre secondo lo stesso, METSCHNIKOFF sosterrebbe che le cellule epiteliali hanno un'origine dalle «cellule embrionali» (mesodermiche?) e le cellule nutrici dalle cellule polari («Polzellen», quindi sessuali), GRIMM sostiene che le cellule nutrici in *Chironomus* derivano, come le epiteliali, dalle embrionali, e pertanto non si possono considerare genitali in senso stretto.

L'idea è da prendere in considerazione se non altro per il fatto che molti anni dopo SOYER, per considerazioni bilologico-generali, e LÉCAILLON, dallo studio dell'ovario di Culicidi, giungeranno a conclusioni alquanto analoghe. Ma, come si dirà in seguito, il problema dell'origine e significato dei diversi tipi cellulari dell'ovario degli Insetti è ancora aperto.

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origine dieversa, non si pronuncia in maniera definitiva. E lo stesso fa Gross (1903) allorchè si limita a citare i lavori degli AA. che sostengono l'idea dualistica. Posteriormente a Giardina, Soyer (1907) studiando l'origine delle cellule follicolari dal punto di vista biologico generale, viene a delle conclusioni alquanto diverse da quelle di Giardina e, si può dire degli AA. in genere. Tale A. osserva ad esempio che in certi casi (*Carpocoris*) cellule follicolari possono indifferentemente evolvere a cellule sessuali, o cellule nutrici o nuove cellule follicolari. Osserva pure che a volte è impossibile distinguere dall'esame microscopico cellule sessuali della camera germinativa («germarium» degli AA. moderni) da cellule che si dispongono a follicolo. Discute indi su basi del tutto (vorrei dire troppo) teoriche sulla possibilità di un'origine comune per le cellule dei diversi tipi presenti nell'ovario di Insetti e conclude alla fine dicendo che le cellule follicolari (tra le quali sembra l'A. voglia includere anche le nutrici!) abbiano un'origine almeno in parte somatica [1].

E' da ricordare accanto a Soyer pure Lécaillon (già citato a proposito della struttura dell'ovario) secondo il quale (1900) la cellula uovo, la cellula nutrice, e le cellule follicolari deriverebbero da cellule sessuali propriamente dette. Egli avrebbe osservato infatti in stadi molto precoci una mancanza di differenziazione tra le stesse, e conclude peretanto (pag. 100): «il faut noter surtout que parmi les cellules sexuelles properment dites il y a une différentiation très accentuée. Certaines de les cellules seules, se transforment en oeufs, alors que les autres ne jouent que de rôles accessoires». (Il lavoro tuttavia non è corredato nè da descrizioni molto accurate, nè da figure, e le affermazioni dell'A. non sono corroborate da dati sperimentali.)

Più recentemente ancora (1929) Chiarugi nel suo trattato di Embriologia dice che il problema se le cellule follicolari abbiano o no un'origine comune colle cellule germinali non è ancora definitivamente risolto.

Prendiamo ora in esame le caratteristiche più degne di nota delle singole categorie cellulari.

Oogoni e oociti sono in genere sempre presenti contemporaneamente in ovari che non hanno raggiunto la completa maturità, e ciò farebbe contrasto colle condizioni del testicolo della stessa specie, dove in genere tutti i nidi fin dall'inizio sono formati di spermatociti I e si evolvono tutti a spermi maturi, senza che si distinguano sicuramente degli spermatogoni. Gli oogoni sono spesso in mitosi, ma il materiale cromosomico è densamente impacchettato e non si presta alla determinazione del cariotipo. Negli oociti il processo della meiosi, che io non ho potuto studiare in tutti i dettagli, decorre per quello che ho potuto osservare, normalmente. Mancano nella parte iniziale della profase stadi «diffusi» (o «confusi», come sono chiamati da alcuni AA. americani recenti) come è il caso per alcuni gruppi di Insetti, e mancano ugualmente stadi di contrazione,

[1] Tali conclusioni, in quanto del tutto isolate, hanno bisogno secondo me di una riconferma.

pure descritti in diversi Insetti. Forse si ha una diffusione del materiale cromatinico durante la fase di diacinesi, dal momento che io non sono riuscito a metter in evidenza delle tetradi; ma d'altra parte non ho nessun motivo per ammetter ciò.

La caratteristica più notevole della meiosi negli oociti della specie di *Chironomus* da me studiata, è lo stadio in cui la cromatina appare a zolle («Kernschollen» degli AA. tedeschi). Tali aspetti del materiale cromatinico hanno riscontro in quelli illustrati da vari AA. tra cui ricorderò BAUER (1933) e WOLFF (1941). Il primo descrive delle «Kernschollen» (che sembrano esser strutturalmente identiche a quelle riscontrate da me in *Chironomus*) negli spermatogoni, negli oogoni, e negli oociti di *Tipula*, il secondo descrive tali aspetti in profasi intermedie di *Phalacrocera replicata*. Il primo A. non si era pronunciato circa la natura di tali strutture, osservando che: «das Material jedes Chromosomenschenkels gesondert erhalten bleibt, dass also die Kernschollen keine ungeordnete Chromosomensubstanz darstellen, sondern mindestens hinsichtlich dieser Trennung zweier Materialbezirke eine bestimmte Ordnung aufzeigen. Über eine Erhaltung der Anordnung der in jedem Schenkel vereinigten Chromatinsubstanz lässt sich natürlich nichts weiter aussagen. Beziehungen zwischen diesen Körnchen und den Leit-körperchen (TRANKOWSKY 1930) und den Insertionsstellen (BELAŘ 1929) die für Chromosomen an derer Heteroplastiden beschrieben sind, lassen sich einstweilen nur vermuten». Tuttavia dice: «In der Art der Chromosomenentstehung aus den Kernschollen lässt sich ein Indicium finden für getrennte Erhaltung der Chromosomenschenkel».

Inoltre BAUER nota la presenza dei seguenti stadi: zolle in riposo: comparsa di corte briglie di cromatina, filamenti continui nelle zolle stesse, ispessimento e aumento di volume del filamento stesso, infine formazione di cromosomi veri e propri (metafase). Dopo lo stadio di zolle si ha secondo BAUER un «Auflockerung» delle zolle stesse.

Nella *Phalacrocera*, studiata da WOLFF [1], negli spermatogoni in riposo il nucleo presenta le tipiche zolle date da diffusione della cromatina (eucromatina). Tale A. considera che le zolle cromatiniche siano date dall'unione di due cromosomi omologhi, e pertanto sono di numero aploide. Da notare che anche le zolle di BAUER erano di numero aploide [2].

In quanto al reperto di BAUER in *Tipula* e al mio in *Chironomus* dirò che in entrambi i casi la formazione cromatinica a zolle si deve

[1] Oltre che in *Phalacrocera* furono trovate delle «Schollen» nella *Scatopse notata*, e precisamente nella profase delle meiosi («Schollenstadium»).

[2] Che le zolle cromatiniche (almeno nella *Phalacrocera*) siano date da eucromatina anzichè, come si potrebbe supporre, da eterocromatina, lo dimostra il fatto che in tale Insetto si notano oltre agli ammassi della cromatina propria delle zolle (numero aploide) pure 2 eterocromosomi (costituiti di eterocromatina), ben staccati dalle zolle stesse (che invece presentano delle lievissime briglie che uniscono le une alle altre) e caratterizzati da un grado di maggior contrazione («packing»).

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interpretare come data da eucromatina. Intanto non tutti i Nematoceri le cui cellule sessuali furono indagate possiedono eterocromatina. Quella che si riscontra in parte è riferibile a cromosomi sessuali (X o Y) in parte a sostanza eterocromatica senza alcuna relazione col cromosoma sessuale. In tale ultimo caso l'eterocromatina rappresenta o una parte del materiale cromatinico legato all'eucromatina (parti di cromosomi) oppure staccata da questi (cromosomi-SAT). In tutti i casi accanto all'eterocromatina c'è dell'eucromatina, rappresentata magari dai soli cromomeri [1]. Non solo, ma non c'è sinora alcuna evidenza che l'eterocromatina proveniente da ciascun cromosoma possa condensarsi in un numero aploide di zolle e costituire un quadro simile a quelli osservati da BAUER e da me, uguali, del resto, a quelli descritti da WOLFF in *Phalacrocera* e *Scatopse*, e interpretati dallo stesso A. come eucromatina.

Abbiamo visto nella parte descrittiva come gli oociti di *Chironomus thummi* in certi momenti dell'evoluzione dell'ovario siano accompagnati da una cellula nutrice. Poco precedentemente si è detto che le cellule nutrici, secondo GIARDINA (e in genere secondo tutti gli AA. più recenti) hanno un'origine comune a quella delle cellule sessuali. GRIMM è stato il primo A. a notare in *Chironomus* la cellula nutrice ed ha stabilito che questa è presente in numero di uno per oocita [2]. Anche GRIMM 1871, conviene con METSCHNIKOFF nell'ammettere un'origine comune per cellule sessuali e cellule nutrici). Tale particolarità sarebbe una eccezione negli Insetti, secondo Eidmann caratteristica solo dei Chironomidi e del genere Forficula.

Un altro A. che si è occupato di tale categoria di cellule è JAWOROWSKI. Secondo questi lo sviluppo dell'ovario nella larva di *Chironomus* dimostra che l'accrescimento dell'uovo non avviene a spese delle cosidette cellule nutrici, ma bensì del sangue.

Confrontando le condizioni presenti in *Chironomus* e quelle che si hanno in altre famiglie di Nematoceri (*Culicidi*, KULAGIN, *Tipula*, GROSS), si nota che in quest'ultimi Insetti le cellule nutrici sono in numero maggiore [3]. Nei *Culex* secondo KULAGIN 3—4 cellule nutrici vengono assorbite dalla cellula ovarica. Ivi il citoplasma si mescola a quello dell'uovo e il nucleo si suddivide in zolle di cromatina.

[1] Farebbe eccezione la *Spirogyra* (descritta da GEITLER 1935) dove secondo BARIGOZZI nel nucleo a riposo si riconoscono solo piccole porzioni eterocromatiche, mentre il resto generalmente non è colorato.

[2] Da notarsi che GRIMM nella sua prima publicazione sull'ovario di *Chironomus* (1870) ha confuso le cellule epiteliali colle nutrici, e per tanto il numero di quest'ultime era ritenuto di molto superiore a 1. Nel lavoro del 1871 l'A. accenna alle cellule nutrici ma ne dà una descrizione solo sommaria, senza soffermarsi a trattare gli intimi dettagli del citoplasma o ancor meno del nucleo. La figura che rappresenta una cellula uovo accompagnata dalla rispettiva nutrice corrisponde abbastanza all'aspetto che presentavano le stesse strutture nel *Chironomus thummi*. Tuttavia non si distinguono i limiti cellulari molto nettamente e non vi è disegnata la cromatina.

[3] Da notarsi che in *Tipula* le cellule nutrici si trovano distalmente all'oocita rispetto al calice ovarico, mentre in Culicidi sono situate prossimalmente.

In genere negli ovarioli dove le cellule nutrici partecipano attivamente all'accrescimento della cellula uovo si hanno condizioni morfologiche particolari anche da parte del nucleo delle cellule nutrici, queste, poi, sec BERLESE presentano «notevoli dimensioni, ciò che da un lato può mettersi in relazione coll'attività secretoria di tali cellule (KORSCHELT), da un altro punto di vista può anche spiegarsi tenendo conto che le cellule vitellogene (nutrici) sono uova abortive (BRUNELLI) ... Caratteristica delle cellule vitellogene è anche la tendenza del nucleo a divenire polimorfo (ramificato, con prolungamenti ecc.) nell'età del massimo sviluppo della cellula ...» BAUER del resto dice che a proposito di *Tipula* l'ovario si può considerare alla stregua di un «panoistische Eiröhr», in quanto «... die Kernvergrösserung lässt den Schluss nicht umgehen, dass die Eizellen zunächst ganz oder vorwiegend aus eigener Kraft wächst und dass die Nährzellen daher eine ihrem Name entsprechende Funktion anscheinend gar nicht ansuben». Del resto credo che anche il numero ridotto di cellule nutrici (una sola, come in *Chironomus* e in *Forficula*) depone per una mancanza di azione trofica di tali elementi.

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Pertanto anche da tali argomentazioni posso dedurre che, come aveva detto ancora l'altro secolo JAWOROWSKI, la cellula nutrice di *Chironomus* non ha funzione nutritiva vera e propria.

Per quello che riguarda le cellule epiteliali si sono già visti quali sono i problemi inerenti alla loro origine e significato. Confrontando i reperti ottenuti da me in *Chironomus* con la descrizione di BAUER in *Tipula*, devo osservare che le cellule chiamate da tale A. «Zwischenzellen» si devono certamente identificare colle cellule che io denomino epiteliali. Tali elementi in *Tipula* secondo la descrizione dell'A. citato non hanno alcuna nota nè funzionale, nè morfologica di interstiziali, se non quella di essere dislocate irregolarmente nell'organo durante i primi stadi dello sviluppo. Da notarsi che secondo BERLESE le cellule interstiziali sono degli elementi che si riscontrano solo a volte negli interstizi delle guaine ovariche. Pertanto io considererei ingiustificata la denominazione di BAUER di «Zwischenzellen». Nei miei preparati non ho mai osservato un aspetto interstiziale di tali elementi, in quanto fin dagli stadi più giovanili della gonade femminile le cellule epiteliali hanno una disposizione di rivestimento, prima degli auxociti, e poi del calice ovarico. Pertanto io ho ancor meno motivi di BAUER per denominarle interstiziali.

CONCLUSIONI.

Il testicolo di *Chironomus* è di tipo unifollicolare o uniloculare. Gli elementi vi si trovano riuniti in gruppi senza però alcun rivestimento cistico. Si nota un relativo sincronismo nello sviluppo dei singoli gruppi.

Gli spermatociti I sono gli elementi più grandi della serie germinale maschile,

e i primi di tali elementi a comparire nella gonade differenziata in senso maschile.

La meiosi è di tipo normale, il primo stadio a comparire ben differenziato essendo quello di pachitene. Mancano stadi di contrazione o di diffusione.

L'ovario è di tipo dieroistico, cioè senza un'evidente suddivisione in ovarioli, sebbene sia il caso di parlare di «catenelle ovariche» («Eikette» degli AA. tedeschi) poste intorno a un calice centrale. Gli oociti in vitellogenesi sono provvisti di una cellula nutrice, la quale però non dimostra di partecipare attivamente al trofismo della cellula-uovo. Il complesso formato dall'oocita e dalla rispettiva cellula nutrice, riuniti in una cisti, è attaccato al calice a mezzo di un peduncolo ovarico.

In ovari di diversa età si notano oogoni accanto a oociti in vitellogenesi più o meno avanzata; gli oogoni sono spesso in mitosi.

La meiosi sembra essere di tipo normale. Vi si notano però solo gli stadi di lepto-e pachitene, nonchè di «Kernschollung» o formazione di «zolle di cromatina». Quest'ultime, che mancano nella serie germinale maschile, sono presenti nelle mitosi di vari elementi sessuali (spermatogoni, spermatociti, oogoni) di parecchi gruppi di Ditteri Nematoceri. Ritengo che tali «zolle» siano costituite di eucromatina anzichè di etrocromatina.

Non si riescono a metter in evidenza tetradi.

SUMMARY.

The structure of the gonads (both male and female) of a species of *Chironomus* (*C. thummi* Kff.) is described. The evolution of the germ-cells from the gonial condition up to the adult stage, is followed, with particular references to the aspect of the nucleus and chromosomes. The following first conclusions are obtained.

The testis of *Chironomus* is of unifollicular (or unilocular) type. The germ-cells are clumped without any formation of cystis. There is a kind of synchronismus in the development of single clumps. Spermatocytes I are the largest cells within the male germ-line, and the first elements appearing in the differentiated gonad. Meiosis is a normal one, its first stage being the pachytene; there are no signs of "contraction", or "diffusion". The ovar is a dieroistic one, though there are, at the place of ovariola, some "ovarial chains" ("Eikette" in German). Oocytes, during the vitellogenesis, are provided with a nurse-cell, which nevertheless has no activity in respect of the ovum. The oocyte plus the nurse-cell, enclosed in cystis, are attached to the ovarial calix ("Eikelch") by a peduncle ("Eistiele"). Also in the female line the meiosis is normal, but the only stages present are leptotene, pachytene and the so-called "Kernschollen"-formation. The last one, present in *Chironomus* only in the female

germ-line, is known for several germ-cells (both male and female) of different Nematocerous Diptera. The Author considers the "Kernschollen" as constituted of euchromatin instead of heterochromatin. No tetrads are seen.

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ON THE DEVELOPMENT AND MORPHOLOGY OF THE SKELETON OF THE HEAD OF PETROMYZON

BY

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I. INTRODUCTION.

As is well known the development of Petromyzon takes place in two stages. The embryonic development results in the appearance of a larva which, after about three years, undergoes a transformation into a full-grown animal. The embryonic stages are fairly well known from different points of view; our knowledge of the later metamorphosis is somewhat incomplete.

The chief part of the present work comprises a study of the transformation of the larval cranium into that of the fully developed Petromyzon. However, opinions in the literature differ regarding the extension of the cranial elements of the larva, particularly of the muco-cartilage. In view of the fact that the definition of this tissue is comparatively vague, an investigation of its microscopic structure was indispensable. The first object was simply to characterize the mucocartilage in order to distinguish this tissue from other connective tissues in Petromyzon. The observations thus made have, to some extent, been applied also to other purposes.

The larval cranium forms the starting-point of the changes during the metamorphosis. For this reason a study of the morphology of the larval cranium has been performed, to serve as a foundation for an analysis of the metamorphosis. Particular attention has been given to the extension of the muco-cartilage.

The cranium of the full-grown Petromyzon consists of cartilage—and, in some degree, of fibrous connective tissue. The development of the different cartilaginous elements has been observed as minutely as the material has permitted. Observations of earlier stages of the metamorphosis—practically missing in the literature—have provided certain indications for judging the origin of the various parts of the skeleton. The available material has also been used for a histological examination of the metamorphosis.

A study of the different cartilaginous elements in the metamorphosed Petromyzon also presupposes an accurate knowledge of the embryonic development. Since this subject has been carefully dealt with by a great many authors, the aim of the present investigation has been simply to supplement and check earlier findings in special respects. However, in view of the

extremely contradictory character of the data recorded in the literature, the origin of the trabecles had to be subjected to a special inquiry.

From the facts emerging from the forementioned investigations an attempt has been made to form an opinion of the relations between the larval and the fully developed cranium of Petromyzon. In this connection, SEWERTZOFF's (1916—17) hypothesis of the occurrence of prebranchial arch elements in the cranium of these animals has been examined. Also, a comparison has been made between the cranium of Petromyzon, on one hand, and those of Myxinoids and Gnathostomes, on the other. In the comprehensive literature on this subject, practically all conceivable views have been expressed. Consequently, the task in the present investigation has, in some degree, been limited to confirming or refuting interpretations previously presented. An attempt has been made to compare the head skeleton of Petromyzon with the endoskeleton of fossil Agnatha principally the best known of these forms, viz., the Cephalaspids.

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This investigation has been performed at the Zootomical Institute of the University of Stockholm. The subject was suggested to me by the former Head of the Institute, emeritus Professor NILS HOLMGREN, who has also very kindly encouraged me in the course of my work and allowed me to benefit by his exceedingly comprehensive zoological knowledge, theoretically as well as methodically. For this I owe him my deepest gratitude. I also wish to record my great obligation to Assistant Professor TORSTEN PEHRSON for valuable help and advice, as well as to Professor P. E. LINDAHL. Finally, I wish to express my deep gratitude to Mr. ROGER WASHBOURN who has had the kindness of reading my manuscript.

II. MATERIAL AND METHOD.

This investigation of the process of metamorphosis has been performed on a material of Petromyzon (Lampetra) planeri, collected and fixed during the months of July, August and September in 1943 and 1944. Larvae have been fixed also at other times of the year, and full-grown animals have been captured during the Spring and early Summer. Certain animals have been kept at an aquarium and fixed in the Winter. In this way also late stages of metamorphosis have been available for examination.

Fixation of these animals has been performed acc. Bouin, Bouin—Allen, Helly, Flemming, Heidenhain, Zenker (ROMEIS 1943) and SMITH (1912), as well as in 90 per cent alcohol, sublimate-formol and "Susa". A number of fixations have been made also acc. Bodian (ROMEIS 1943).

The material has been embedded in paraffin and sectioned in series with sections in most cases 10 μ, occasionally 15 μ in thickness.

The preparations have been stained in azan-Mallory (Heidenhain), Bismarck brown-bleu de Lyon, iron-trioxyhematein-picrofuchsin, iron trioxyhematein-eosin, iron-trioxyhematein-Bismarck brown-bleu de Lyon, iron-hematoxylin-picrofuchsin and acc. Bodian (ROMEIS 1943). The staining methods used on histological material will appear from Chapter III. They have been applied according to ROMEIS' (1943) directions.

In connection with the histological examination of the muco-cartilage, fresh material has been examined in the polarization microscope and the phase contrast microscope. Further, a special smearing technique has been employed for a particular purpose, involving the preparation of small pieces of muco-cartilage in a physiological salt solution and their placing on an object glass. A cover glass, to the underneath side of which a drop of a suitable fixation fluid has been added, is then placed over the object glass in such a way as to immerse the piece of muco-cartilage in the fixation fluid. This piece is then rapidly crushed by the application of a suitable pressure on the cover glass. Provided the latter, before the beginning of the proceeding, has been thinly overlaid with fat, it can be removed in alcohol. The preparation can then be stained as desired.

The embryological material—consisting of Petromyzon (Lampetra) fluviatilis—comprises a series of stages from the cleavage of the egg to the transformation into young larvae. It has been fixed acc. Bouin, Helly and SMITH (1912). This material also was embedded in paraffin and sectioned in series, the thickness of the sections being, as a rule, 5 μ. The staining has been performed in azan-Mallory (Heidenhain) and acc. DAMAS (1945). By using SMITH's fixation fluid, extremely distinct preparations will be obtained, since, by this method, the difficulties that most often attend a staining of material rich in yolk (cf., e.g. DAMAS 1944, 1945) have, on the whole, been eliminated.

The analysed material in the present investigation includes the following series: More than 100 embryonic specimens, 22 larvae, 28 stages of metamorphosis and 3 full-grown animals. In addition, the large collection of preparations belonging to the Zootomical Institute has been available.

For the most part, the reconstructions of skeletal parts have been graphic. In two cases, however, plastic reconstructions have been made by means of wax plates.

III. THE SKELETON OF THE LARVAL HEAD.

Cartilage occurs only to a relatively slight extent in the larva of Petromyzon. Nevertheless, both muco-cartilage, a tissue first noticed by SCHNEIDER (1879), and fibrous connective tissue have to be counted among the elements that form the cranium. The histological structure of the fibrous connective tissue and

the cartilage has, in the main, for long been well known (SCHAFFER 1896, 1897, 1901, 1903, 1906, 1930, STUDNIČKA 1897, 1898 a, 1898 b, 1903, HANSEN 1905, and others). On the other hand, data from literature regarding the finer structure of the muco-cartilage, as well as its extension, vary considerably. The differences in the former instance have, very likely, at least partly, formed the origin of those in the latter case. An examination of the histology of the muco-cartilage, therefore, was a prerequisite for a study of the larval cranium.

1. THE HISTOLOGICAL STRUCTURE OF MUCO-CARTILAGE.

Like any cartilage, the muco-cartilage is, according to SCHNEIDER (1879), enveloped by a special surface membrane, a "perichondrium". He writes (p. 43) as follows: "Die Platten des Perichondrium weichen auseinander und lassen einen Raum zwischen sich, welcher fast ganz mit Fäden ausgefüllt wird, welche vorherrschend senkrecht zu den Platten des Perichondrium stehen, aber auch in allen andern Richtungen verlaufen. — — — Auf den Fäden liegen sternförmige Bindegewebszellen. Zwischen den Fäden und Zellen befindet sich keine feste Interzellularsubstanz sondern Flüssigkeit." KAENSCHE (1890) stated that the obliquely proceeding fibres combine the different cells into a network.

According to these data the muco-cartilage is, thus, characterized by three main elements, viz., fibres, cells, and intercellular substance.

a. *The intercellular substance.*

The intercellular substance was interpreted by SCHNEIDER (1879) as more or less liquid. After careful examinations SCHAFFER (1896) and STUDNIČKA (1897) arrived at the opinion that the muco-cartilage gave a chondromucoid reaction. GASKELL (1900) drew attention to its "staining reaction with thionin". TRETJAKOFF (1927 c) performed various examinations in accordance with HANSEN's classic investigations of cartilage (1905), classifying the muco-cartilage as a type of tissue which he called "das basophile Gallertgewebe". One of the properties of this tissue is "die Basophilie der gallertigen Grundsubstanz". He writes (p. 39) as follows: "Die Basophilie tritt im Schleimknorpel bei genau denselben Bedingungen auf, wie überhaupt im basophilem Gallertgewebe. Der Schleimknorpel des Ammocoetes ist also eine Abart des Basophiles Gallertgewebes, kein Knorpel." However, in the introduction to the same work, he observes (p. 30): "Die Basophilie des Gallertgewebes wird genau bei denselben Bedingungen bemerkbar, wie die Basophilie der Knorpelgrundsubstanz." Thus, also TRETJAKOFF notes considerable conformities in the matrix in the muco-cartilage and the cartilage, respectively. A summary of the literature on this subject can be found in SCHAFFER's work (1930).

In the present investigation the structure and stainability of the intercellular

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substance have been noticed to be greatly susceptible to unsuitable fixation substances. According to our experience a satisfactory result will be secured by fixation acc. Bouin. Also Helly's fluid and sublimate-formol produce acceptable results, while fixations acc. Heidenhain ("Susa", etc.) succeed less well. On the other hand all the fixatives containing chrome, tried in the present connection, have had a greatly disturbing influence, as a rule causing the matrix to shrivel and crack. In addition, its stainability becomes markedly reduced, or it disappears totally, as in the case of the matrix of hyaline cartilage (HANSEN 1905). These facts have, probably, in the past contributed to several misinterpretations, as will be seen from observations recorded later.

Provided that the matrix has not been damaged at fixation, an intense colour can be obtained by means of a great many stains, such as muco-hematein, mucicarmine, Bismarck brown, methylene blue, toluidine blue and thionin. The three last-mentioned stains colour the matrix metachromatically, thionin producing the most intense result. According to LISON (1935), metachromatic staining would indicate the presence of a special sulphuric acid compound, occurring, inter alia, in the form of chondroitin sulphuric acid in the cartilage. The intercellular substance will also be strongly stained by orcein and resorcin fuchsin, dyes which are generally used for the purpose of determining the occurrence of elastic connective tissue (see below).

In his standard work concerning the histology of the cartilaginous tissue, HANSEN (1905) has devoted a minute study to the properties typical of the matrix of the cartilage. Certain experiments have, in the course of the present investigation, been performed with a view to ascertaining whether the muco-cartilage offers any similarities to cartilage. It is evident that the intercellular substance in the muco-cartilage—like the hyaline cartilage—can be removed by treatment with acid or alkaline solutions. Still, a certain difference in the rapidity of the reaction is noticeable between cartilage and muco-cartilage. As soon as after one hour's treatment with 1.5 per cent of a KOH solution every trace of basophilia was found to be missing in the cartilage (trabecles, auditory capsules), while, as late as after three hours, the muco-cartilage, if stained with toluidine blue disclosed a conspicuous, though faint, metachromatic tint. In the case of certain stainings a similar phenomenon is observed. Thus, the cartilaginous elements will dye with extreme rapidity with for example, Bismarck brown, while the muco-cartilage will assume the same degree of staining as that of the cartilage only after a considerable lapse of time. These differences may very conceivably be due to differences in the chemical composition in these two cases. However, they can be explained also in another way. Considering the comparatively low rate of rapidity that is characteristic of these reactions, the structural difference between cartilage and muco-cartilage may play an essential part. Because of the subdivision of the cartilage, this tissue is more easily accessible to reagents than the more compact mass of the muco-cartilage.

b. *The fibres of muco-cartilage.*

The differences in opinion of the various authors are particularly accentuated with regard to the nature of the fibres of the muco-cartilage. SCHNEIDER (1879), BUJOR (1890—92) and DAMAS (1935, 1944) describe these as being elastic, while, on the other hand, SCHAFFER (1896, 1930) found several reasons for classifying them as collagenous fibres of connective tissue, an opinion apparently adopted also by TRETJAKOFF (1929a). STUDNIČKA (1907) calls them tonofibrils.

SCHNEIDER (1879) based his view of the elastic nature of the muco-cartilaginous fibres on the fact that these fibres fail to produce any swelling when treated with cold acetic acid. SCHAFFER (1896) who, after experiments of his own, arrived at a diametrically opposite view suggests that SCHNEIDER must have made some mistake in his method which led him into his erroneous conclusion. The control experiments performed in the present investigation disclose an evident deformation of the fibrous elements that form part of the muco-cartilage, when treated with cold, diluted acetic acid. Thus, in this respect the muco-cartilaginous fibres do not reveal any similarity to elastic fibres.

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SCHAFFER rejects the possibility of ascertaining the elastic nature of the muco-cartilaginous fibres by means of orcein and other "specific" elastin dyes. DAMAS (1935, 1944), who does not mention SCHAFFER's work in his list of literature, speaks, however, of "des fibrilles élastique anastomosées" which he, according to his own statement, has stained specifically with orcein.

The present staining experiments, carried out in order to verify these data, have failed to produce elastin staining of the fibres of the muco-cartilage with orcein acc. Unna, resorcinol fuchsin acc. Weigert, elastin H. acc. Hollborn and acc. van Gieson. With orcein and resorcin-fuchsin these staining methods are unsuccessful on not specially treated material, this because of the fact, if for no other reason, that the matrix, as previously mentioned, when undamaged in the fixation, assumes a markedly intense tint, thus blotting out other details. In the preparations referred to by DAMAS, the intercellular substance must, in some way or other, have been destroyed. The remains may have left an impression of "specifically" stained elastic fibres. However, preparations treated acc. HANSEN, in order to remove the intercellular substance, are stainable without the appearance of this disturbance. True, a staining of the remaining structures of the muco-cartilage will be obtained with resorcin-fuchsin and orcein, as well as, it may be added, with methylene blue and toluidine blue (though not metachromatically) and muco-hematein, but any difference with regard to the collagen is hardly, in these instances, detectable.

TRETJAKOFF (1927c) states that the fibres of the muco-cartilage "sich zu den Färbemitteln fast ebenso wie kollagene Fasern verhalten. Ihre Tin-

gierung erreicht aber niemals den Grad der Färbung echter kollagener Fasern." The correctness of this statement has been confirmed in the present experiments by staining with, for instance, Mallory's azan-stain (modified by Heidenhain) or with picro-fuchsin acc. HANSEN. This is most easily noticeable in the places where the collagenous fibres appear in a direct contact with the muco-cartilage, e.g., in the superficial layer, where collagenous fibres often form a sort of perichondrium, or in the rostral or caudal parts of the ventro-lateral plate, where such fibres often intersect the muco-cartilage itself. Preparations that have not been subjected to any treatment for the removal of the intercellular substance (acc. HANSEN) reveal a distinct difference in staining between the collagenous and the muco-cartilaginous fibres. The latter are fainter, mostly rather diffusely tinted, while the collagen is characterized by a clear, strong colour. The difference appears to be more accentuated after a treatment of the preparations with alkaline solutions.

An even more marked difference between the collagenous and the muco-cartilaginous fibres is obtained by staining with Congo red acc. Matsuura. According to the description the collagen becomes blue, while the fibres of the muco-cartilage remain diffusely red.

Attempts to ascertain a similarity to the fibres of reticular connective tissue, acc. Bielschowsky, failed. The result of these staining experiments appear to show a certain individuality of the muco-cartilaginous fibres in comparison with any of the three groups of connective tissue fibres.

TRETJAKOFF (1927 c) refers to yet another element in the tissue of the muco-cartilage. He writes as follows: "Ausser den aufsteigenden Fasern ist an Stelle der Grundsubstanz ein aus feinsten basophilen Fädchen zusammengesetztes Filzwerk vorhanden. Die Fädchen zeigen in ihrem Verlauf keine bestimmte Orientierung" (p. 39). He claims to have noticed fine pictures of these fibres in preparations stained, for the purpose of a study of the nerves, acc. R. y Cajal. Neither with the Cajal method nor with any other silver impregnation methods (acc. Bielschowsky and Bodian) have these formations proved detectable in the present experiments. One explanation can be that TRETJAKOFF has happened to describe artificial products in the matrix. In view of the lack of reliability of the method he adopted, this possibility cannot be altogether excluded.

Opinions also differ with regard to the shape of the muco-cartilaginous fibres. Thus, SCHAFFER (1896) reports that the fibres "legen sich, wenn sie entspannt werden, in korkzieherartige Windungen". STUDNIČKA's figures (1907) confirm this observation, a fact mentioned also by DAMAS (1935). TRETJAKOFF (1929 a) makes the following contrasting statement: "Nach meinen Beobachtungen verlaufen sie meistens gerade".

According to the observations in the present investigation, the above-mentioned spiral twist of the muco-cartilaginous fibres does not appear in

fresh material, not even in small pieces of muco-cartilage torn from it, in which the fibres have slackened. On the other hand, the cork-screw curl will appear regularly in material fixed, e.g., acc. Bouin, Helly or with sublimate-formol. It occurs chiefly in the muco-cartilage in the ventro-lateral plate and the central part of the rostro-dorsal plate. At any rate, it has not in the present investigation been observed within any other areas.

General remarks to the effect that the muco-cartilaginous fibres differ in shape, as well as in their local orientation in the various places where they occur, have been made by several authors (Bujor 1890—92, Schaffer 1896, Tretjakoff 1927 c). Studnička (1897) writes as follows (p. 635): "Die Schleimknorpel sind manchmal sehr dicht gebaut; die Fibrillen sind dicht an einander, in anderen Fällen sind sie sehr locker und auch sehr unregelmässig angeordnet, besonders dann, wenn keine 'Perichondrien' vorhanden sind." In many parts of the mass of the muco-cartilage it is, therefore, impossible to distinguish any principal direction in the orientation of the muco-cartilaginous fibres. Only within the ventro-lateral plate, the central part of the rostro-dorsal plate and round the pedicles can such a trend be noticed. Here the fibres are for the most part arranged perpendicularly to the surface of the "perichondria". In addition, they are more densely collected here than in other places. Also the nuclei of the cells lie more closely than otherwise in the muco-cartilage. For these particular reasons the muco-cartilage in these places lends itself less easily to observations. Thin sections show, as a rule, only fractions of the different elements while thicker ones defy examination on account of the accumulation of different cellular elements. To this has to be added the obscuration inherent in most staining methods, as far as the intercellular substances is concerned.

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c. *The cells of muco-cartilage.*

Authors who have dealt with the histology of the muco-cartilage have almost without exception made a sharp distinction between the muco-cartilaginous fibres and the processes of the muco-cartilaginous cells. Schneider (1879) formulates his views as follows: "Auf den Fäden liegen sternförmige Bindegewebszellen." Bujor (1890—92) is of a similar opinion. Schaffer (1895, 1896) endeavoured to demonstrate the identity in the processes of formation of the muco-cartilaginous fibres and ordinary connective tissue fibrils which, according to results of Lwoff (1889) and others, are to be interpreted as intercellular formations. Schaffer based his conclusion regarding this matter on examinations both of sectioned and of fresh material and, finally, also on analyses of material hardened in Müller's fluid. In the latter instance small pieces of muco-cartilage were stained in eosin and Congo red and after that "sorgfältig zerzupft". He records his observations in the

following words: "Zwischen den Fasern treten nun deutlich verästelte Zellen mit faden- oder flügelförmigen Fortsätzen hervor, welche vielfach unter einander zu anastomosieren scheinen" (p. 638). He adds: "Die Beobachtung dieser Anastomosen wird einigermassen dadurch erschwert, dass die Zellausläufer sich oft sehr stark abplatten, verbreitern und anscheinend aufgefasert ganz allmählich in die Grundsubstanz verlieren. — — — Auffallenderweise gelingt es nie solche anastomosierende Zellen vollkommen zu isolieren; Betrachtet man dieselben aufmerksam mit den stärksten Vergrösserungen, dann sieht man zwischen ihren Ausläufern und dem Zelleib dünnste Häutchen ausgespannt, und in diese Häutchen, nicht in formlose Grundsubstanz, verlieren sich auch die aufgefaserten Enden der Zellen" (p. 640). In the surface layer of these lamellae SCHAFFER noticed certain fibrillar structures, the course of which could be followed over the cellular bodies and further out over other membranes. With this in view he writes as follows (p. 640): "Diese letzte Beobachtung, — — —, bewahrt uns auch vor der irrthümlichen Annahme, als ob hier die platten, zerfaserten enden der Zellen direkt in die differenzirten Fibrillen übergehen würden, d. h. als ob letztere aus den Ausläufern der Zelle auswachsen würden." Opinions expressed by TRETJAKOFF (1927 c) and DAMAS (1935) do not differ from those quoted above. Only STUDNIČKA (1897), otherwise in agreement with SCHAFFER's results, expresses a divergent opinion, stating (p. 635): "Die Fibrillen sind von den Fortsätzen der Zellen kaum zu unterscheiden."

It seems likely that some of the detailed observations, recorded by SCHAFFER, can be explained as artificial products deriving from the use of Müller's chromatic fluid. This applies to the thin lamellae and to the fibrillar structures noticed by SCHAFFER on the surfaces of the cells and the lamellae. In the present investigation a collapsed intercellular substance has often been seen to adhere to cells and processes of cells in the case of unsuitably fixed material.

As far as ascertainable in the present experiments all the elements that form part of the muco-cartilage are observable in fresh material, on account of the prevailing light refractions. Distinct pictures are obtained when using a so-called phase-contrast microscope. The same structures are to be found on a suitably fixed material while the forementioned chromatic fixations cause considerable changes in the matrix.

Sections through other parts than the ventro-lateral plate, e.g., the lateral mouth plate, the lateral part of the rostro-dorsal plate or the subotic portions of muco-cartilage, do not give the impression of a regular fibrillar tissue. By suitable staining, for instance by Mallory's azan-dye or picrofuchsin acc. HANSEN, the muco-cartilage in these areas appears to consist of a rather irregular, more distinctly coloured network, surrounded by a faintly tinted intercellular substance. The fibres in this network vary greatly in shape and thickness. While being in one place thick and fibrillar, they are in another transformed into

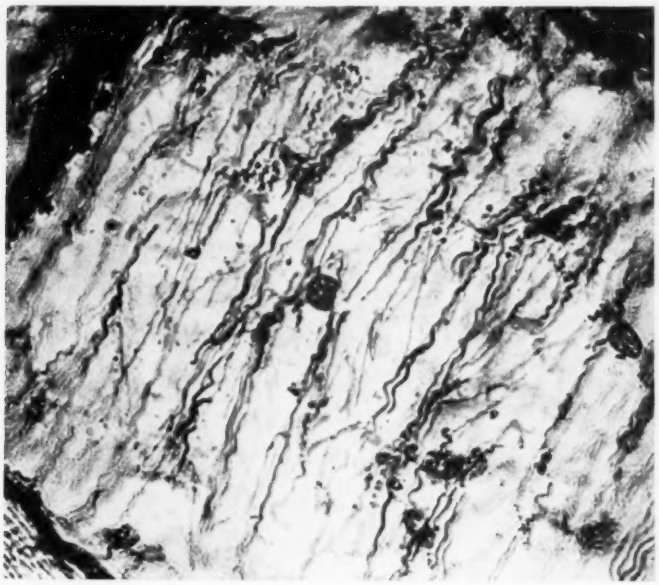

Fig. 1. Section through the lateral rim of the ventro-lateral plate. Larva 116 mm. In the middle a nucleus. Cell processes projecting perpendicularly towards the perichondrium. The perichondrium in the upper right and the lower left corner. Bouin, azan-Mallory. 10 μ. 890 ×.

broad lamellae. The relatively thinly scattered nuclei will always appear in connection with these fibres. When the fibres are long and narrow the nuclei in their interior are fairly longitudinal, while in larger accumulations of plasma they tend to become rounded. Most frequently they are faintly ovoid. The greater part of the plasma in the fibres is, as a rule, collected round the nuclei.

In the ventro-lateral plate, the fibrous elements (fig. 1) are principally perpendicular to the surface of the "perichondria". The difficulty of obtaining an idea of the structure of the muco-cartilage in the ventro-lateral plate could to some extent be overcome by using the previously mentioned smearing technique. Thus, a preparation is obtained where the cells and their processes are made to spread in one plane. With a suitable pressure no more severe cracks will occur, and even though these preparations fail to disclose the mutual orientation of the various elements, such elements as are developed will be distinctly visible. Also in the ventro-lateral plate the fibrous elements seem to be simply processes of cells, however much their accumulation and regular arrangement may leave an impression of a specific differentiation of the muco-cartilage in this area.

Preparations stained with azan acc. Mallory show that the plasma in the vicinity of the nuclei assumes a faint red. In places where a nucleus has been sectioned in two halves, or is situated very close to the surface, this staining

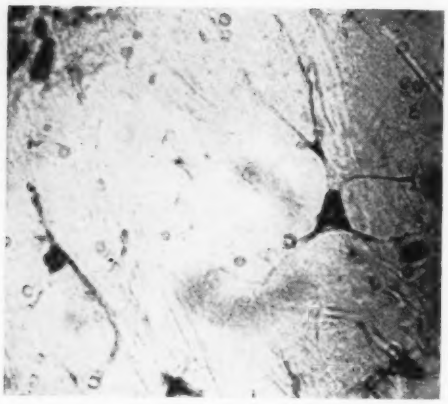

Fig. 2. Section through the ventro-lateral plate. Nucleus and endoplasm dark. Ectoplasm of the cells and cell processes not stained but visible because of light refraction. Bodian. 10 μ. 890 ×.

is found to be limited to the central parts of the plasma, i.e. those situated closest to the nucleus, while, in the periphery, the plasma has a blue colour. Plasma fibres and membranes situated more distally to the nucleus disclose, on the other hand, a more homogenous blue. In preparations stained acc. Bodian, with a view to nerve examinations (fig. 2), the plasma situated nearest to the nucleus had, in certain instances, blackened, while the parts that, in the previous case, had become blue remained colourless. Nevertheless, the fibres in the preparation proved distinguishable on account of their pronounced capacity of light refraction. From experiments in a polarization microscope, elements capable of a double refraction have been seen to form part of the plasmatic and fibrous network. The above observations may lead to a supposition that the plasma immediately surrounding the nuclei constitutes a sort of endoplasm, peripherally surrounded by an ectoplasm. It seems, however, likely that this capacity of double light refraction is confined to the ectoplasm, since it forms the chief part of all the fibrillar cell processes. Thus, a regular fine structure, such as a double refraction capacity is supposed to indicate, common to mechanically active tissue elements, would be characteristic of the ectoplasm of the cells.

d. *The histogenesis of muco-cartilage.*

The first data regarding the development of muco-cartilage are to be found in STUDNIČKA's work (1907): "An gut fixierten und mit Eisenhämatoxylin-Bordeaux R. gefärbten Präparaten von jungen, etwa 12 mm langen Larven von Petromyzon fluviatilis findet man in den vordersten Brustgegend (Querschnitte, die oben die Höhrkapsel getroffen haben) an der Oberfläche des Körpers zuerst die, zu der Zeit noch einschichtige Epidermis, — — — Unmittelbar unter der Epidermis findet man eine intensiv gefärbte dünne Lamelle, die der Anlage des Coriums entspricht. Erst unter dieser befindet sich das embryonale Mesenchymgewebe. — — — An dem — — — Präparate liegen die Zellen, schon etwas weiter von einander und sind mittels reichlich sich verzweigender Fortsätze überall in Zusammenhange. Man könnte da von einem protoplasmatischen Netze sprechen, in dessen Maschen die Zell-

kerne eingelagert sind, — — —. Eine Grundsubstanz kommt in diesem Stadium noch nicht vor; Leere Interzellularlücken trennen die Zellen voneinander" (p. 505). The intercellular substance, at this stage apparently liquid, had not attracted any attention, while such a substance, characterized as "etwa schaumartig", is referred to in an immediately following passage. Here STUDNIČKA records the occurrence of muco-cartilaginous fibres. He terms them tonofibrils.

According to DAMAS (1944) the preponderant part of the connective tissue and skeletal elements of the head—a subject to be dealt with later—originates from cells derived from ectodermal placodes. This ectomesoderm (the term acc. PLATT 1893) first appears as isolated cells which, in the course of development, will form a cohesive complex primordium. Towards the end of the embryonic development these cells will form a continuous mass in which other organs and primordia will lie more or less embedded. DAMAS (1944, p. 210) writes: "Les cellules mésectodermiques conservent très longtemps un aspect embryonnaire: protoplasme condensé, noyaux volumineux. Très tôt, elles ont utilisé leurs plaquettes vitellines, ce qui permet souvent de les distinguer du mésoblaste. Au moment où les tissus de la larve commencent à prendre leur aspect définitif, le mésectoderme se spécialise lui aussi. Il donne naissance à du tissu conjonctif, aux enveloppes du système nerveux, à des cellules pigmentaires, à des pièces cartilagineuses et surtout à ce tissu élastique d'aspect chondroide, special à l'Ammocète, — — —." The embryonic character will remain for the longest time in cells that form the muco-cartilage. Only in a 5 mm long embryo will certain parts begin to change their histological structure. DAMAS writes as follows (p. 147): "Les limites cellulaires disparaissent, les noyaux deviennant sphériques, s'écatrent les uns des autres. Entre eux apparaît une substance fondamentale assez abondante qui fait contraster très fort l'aspect actuel du tissu avec celui qu'il avait au stade précédent." In a 6 mm long embryo the tissue begins to resemble "la structure du tissue élastique d'aspect chondroide", while, in 8 mm embryos, the boundary between this tissue and other kinds of connective tissue remains vague. In 12 mm long specimens DAMAS noted—as did STUDNIČKA—muco-cartilaginous fibres, "abondantes mais n'ont pas encore cet aspect sinueux qui les caractérise chez la grande larve", to quote DAMAS. He adds: "Cette évolution histologique va de pair avec une réduction de l'espace occupé par le tissu."

From this it will be evident that the histogenesis of muco-cartilage is a long-protracted process. Among the typical elements of the muco-cartilage the intercellular substance develops first. Then the cells and their processes are successively transformed into typical muco-cartilaginous elements. It remains a matter of some doubt wether typical muco-cartilaginous fibres have developed as early as at the 12 mm stage. In larvae of a length of abouth 30 mm, the muco-cartilage in the ventro-lateral plate is little differentiated, as far as the fibres are concerned. Anyhow, such histological conditions as are described in

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the literature are only to be found in larger specimens. The degree of development of the mechanical elements in the muco-cartilage appears to be intimately related to the size of the animal.

According to the above-mentioned data regarding the finer structure and development of muco-cartilage, this tissue consists of cells characterized by long processes. These frequently come into contact with similar branches from other cells. They are often, or perhaps always, especially differentiated for a mechanical function. The various cellular elements are enveloped by a gelatinous matrix. In view of these facts it seems only natural that the muco-cartilaginous fibres stain differently from other connective tissue fibres, with which they apparently do not show any close affinity.

2. DESCRIPTION OF THE CRANIUM.

a. *The fibrous elements.*

The brain capsule consists chiefly of fibrous connective tissue. Rostrally it is connected with the caudal parts of the nasal capsule and, ventro-laterally, with the trabecles and the parachordals. The connective tissue membrane in the basicranial fenestra is well developed. It surrounds caudally the projecting notochordal tip. The fibrous brain capsule is also attached to the medial sides of the auditory capsules. Caudally to these points of attachment the brain capsule continues caudad as a protection for the spinal cord. Rostrally it is connected with the parachordals and caudally with the dorsal surface of the notochord. The connective tissue capsule surrounding the orbit joins the lateral surface of the brain capsule medially. These conditions have, on the whole, been described previously by RATHKE (1826—27) and MÜLLER (1834).

b. *The cartilaginous elements.*

The main features of the cartilaginous elements forming the skull of the Petromyzon larva (fig. 3) have long been known. RATHKE (1826—27) disclosed important characteristics in the structure of, mainly, the branchial basket and the auditory capsules. His report was supplemented in several respects by MÜLLER (1834) who, inter alia, demonstrated the cartilaginous elements included in the cranial basis which, in his opinion, were homologous with those in the cranial basis of other vertebrates. LANGERHANS (1873) discovered the existence of a nasal capsule of cartilage and of the pedicles, projecting laterally from the cranial basis on a level with the rostral part of the auditory capsule (cf. PARKER 1883). However, it should be emphasized that RATHKE (1826—27, p. 76) speaks of a small process "des Brustgerippes, welcher sich an den Schädel zwischen der Gehöhrkapsel und der

Augenhöhle ansetzt, — — —". This formation, erroneously interpreted by RATHKE as cartilage in its entire extent, seems to have involved also the pedicle. NESTLER (1890) and SCHAFFER (1896) have later contributed much to a deeper knowledge of, principally, the structure of the branchial basket. Apart from the forementioned authors, several others have more or less closely dealt with questions relating to this subject (AGASSIZ 1835—43, SCHULZE 1856, HUXLEY 1875—76, CALBERLA 1877, SCHNEIDER 1879, KAENSCHE 1890, BUJOR 1890—92, SCHAFFER 1895, 1896, GASKELL 1900, SEWERTZOFF 1913,

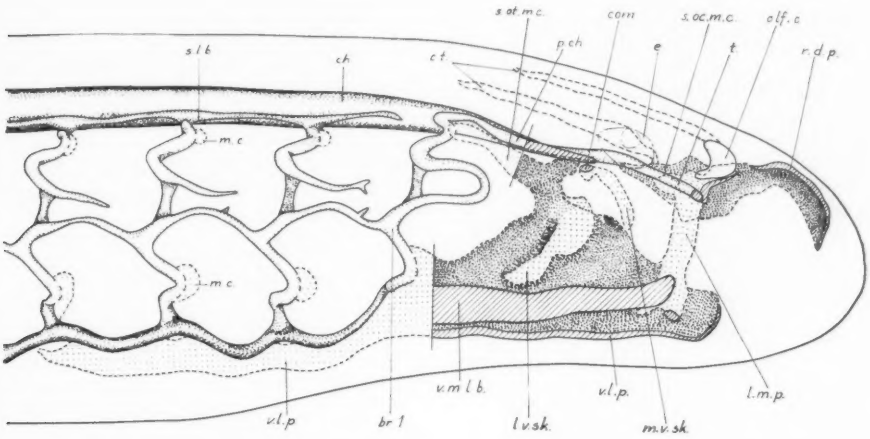

Fig. 3. Larva, 128 mm. Reconstruction of the skeleton of the head. The branchial part in lateral view, the rostral part in sagittal section. Auditory capsule and the muco-cartilage of the side lip omitted. The connective tissue of the dorsal myoseptum and ventrally to the musculus supraocularis (*c.t.*) is shown. Sectioned surfaces obliquely striped. 8 ×.

1916—17, SCHALK 1913, TRETJAKOFF 1929 a, BALABAI 1935, DAMAS 1935, 1944, HOLMGREN and STENSIÖ 1936). The following description is based partly on information obtained from these investigators and partly on own observations, some results of which have been published earlier (JOHNELS 1944).

The cartilaginous elements forming the neural cranium are comparatively sparse. Only the parachordals, the trabecles, the pedicle processes (which are not, as a rule, considered to belong to the neural cranium in the true sense, cf., however, HOLMGREN 1946), and the auditory and nasal capsules consist of this material.

The parachordals, which are closely attached to the notochord, are thin rods rounded in transverse sections but flattened against the notochord. Caudally they are in direct contact with the branchial basket (see below). Rostrally they pass without any visible border-line into the trabecles, the latter being also long, thin rods, practically circular in shape, when seen in transverse section. The boundary between these formations can, on the basis of previous stages of

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development, be assumed to lie caudally to the laterally directed pedicle process. This process is, in larvae that have passed the embryonic stage, situated ventrally to the rostral part of the auditory capsule, immediately laterally to the place where the tip of the notochord projects between the rostro-laterally directed trabecles. The latter then proceed rostral, finally to unite in the trabecular commissure. The free notochordal tip projects further into the basicranial fenestra in young than in old larvae.

The auditory capsules are longitudinal ellipsoid structures. Their ventral surfaces lie on a level with the parachordals with which they are connected by means of strong, dorso-ventrally flattened bars. Dorsally to these bars, the medial sides of the auditory capsules are perforated by a large hole. An additional small foramen for the exit of the facial nerve is to be noted on the ventral side, rostrally to the medial orifice (SCHNEIDER 1879). The chiefly fibrous nasal capsule is reinforced by two lateral, dorsally connected, cartilaginous arches which are convex in a rostro-lateral direction.

The visceral cranium consists of a system of mutually connected, slender cartilaginous rods. Broadly speaking, it can be described as a network, comprising on either side seven transversal branchial arches and four longitudinal rods that more or less completely unite the former with each other. The longitudinal rods are referred to by the present author, in conformity with SCHAFFER (1896), according to their position, as the subchordal, the epitrematic, the hypotrematic and the ventral longitudinal bars, respectively.

A transversal branchial arch includes a dorsal epitrematic part and a ventral hypotrematic one. These two parts, consisting of cartilaginous bars with complicated curvatures, are united on a level with the gill slit through a medially convex, strong cartilaginous arch.

Where the ventral longitudinal bar joins each branchial arch it makes a dorsally convex curve. Rostrally the ventral longitudinal bar passes into the first branchial arch and caudally into the seventh. On a level with the fifth, sixth and seventh gill pockets, the two longitudinal bars meet ventrally in the median line where they fuse for a short space. Rostrally to the fifth gill sac they run separately on either side of the thyroid gland.

The hypotrematic longitudinal bar is formed by a series of cartilaginous rods connecting the different branchial arches with each other, ventrally to the gill slits. The rod, coming from a caudal direction, connects with the branchial arch slightly caudo-ventrally to the place from where the rostral extension of the same longitudinal bar issues.

The epitrematic longitudinal bar—situated dorsally to the gill slits—is formed by separate rostrally directed cartilaginous processes, one from each branchial arch. The parts of the epi- and hypotrematic longitudinal bars lying between the first and the second and between the second and the third branchial arches have, rostrally to the appertaining gill slit, one ventrally and one dorsally

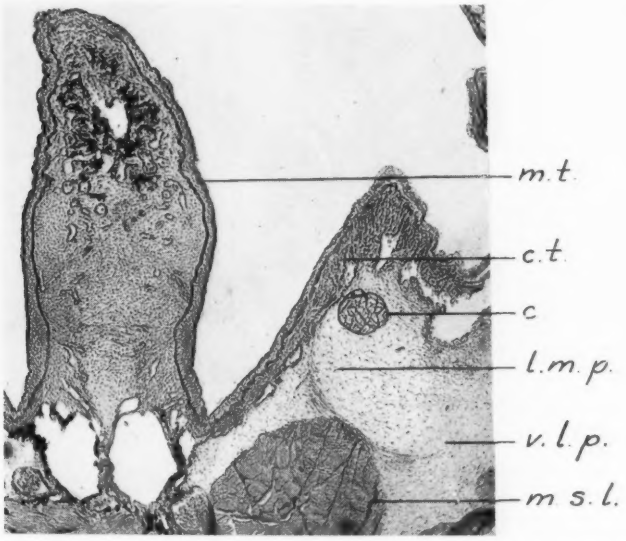

Fig. 4. Larva, 103 mm. Transversal section through the medial tentacle and the ventro-lateral part of the lateral mouth plate. 100 ×.

directed cartilaginous process, respectively. Sometimes there are two processes on each longitudinal bar. Occasionally there are no such processes developed (cf. SCHAFFER 1896, pl. XVIII, figs. 3 and 4). The first gill slit is entirely surrounded by a cartilaginous loop.

The subchordal longitudinal bar connects the dorsal parts of the branchial arches, from the seventh to the second arch. From the latter, it extends further rostrad, though without reaching the first branchial arch. In the rostral part the subchordal longitudinal bar fuses with the latero-ventral surface of the notochord. Caudad this attachment becomes gradually less intimate. The caudal half of the subchordal bar is free from the notochord and situated ventrally to it and laterally to the dorsal aorta. On a level with each arch, the subchordal longitudinal bar is thickened, having in these parts a triangular transverse section where the longest side is attached to the notochord. SCHAFFER (1896) observed a case where the bars had met on the ventral side of the notochord. Between the branchial arches the subchordal longitudinal bar is thinner and connected with the notochord more latero-dorsally. In this manner, it continues as a series of dorsally convex curved pieces between the branchial arches.

The first branchial arch has, as previously mentioned, no caudal connection with the subchordal longitudinal bar. Dorsally it joins, instead, the caudal end of the parachordal cartilage. This causes a fusion with the side of the notochord more dorsally than in the case of the posterior branchial arches (SHIPLEY 1886—87). The caudal end of the parachordal cartilage borders upon the

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dorsolateral surface of the notochord. DAMAS (1944) observed a case where the dorsal end of the first branchial arch was separated from the parachordal. Unfortunately, the exact position of this gap is not stated.

SCHAFFER (1896) reports that he found a piece of cartilage in the dorso-caudal part of the muco-cartilaginous ventro-lateral plate. Also the present author has in two cases observed cartilaginous elements in the muco-cartilage, though, in both these instances, in the ventral part of the lateral mouth plate. In one case, the cartilage had formed only on one side (fig. 4), in the other on both (figs. 32, 34). However, there will be occasion to return to these matters later.

c. *The muco-cartilaginous elements.*

The above-mentioned cartilaginous formations in the skull of the larva are supplemented by muco-cartilage which has its greatest extension in the rostral parts of the head (fig. 3). As early as in 1827, RATHKE mentioned a special "Zellgewebe" which was stated to occur in several places in the head (e.g. in the upper and lower lips and in the ventro-medial tentacle). The actual discovery of the muco-cartilage is, however, attributed to SCHNEIDER (1879) who, in a morphological and histological investigation, demonstrated its significance as one of the elements forming the cranium. Later, a number of authors have subjected the muco-cartilage, and related problems, to discussion (KAENSCHE 1890, NESTLER 1890, BUJOR 1890—92, SCHAFFER 1895, 1896, GASKELL 1900, SEWERTZOFF 1916—17, STENSIÖ 1927, TRETJAKOFF 1927 c, 1929 a, BALABAI 1935, DAMAS 1935, 1944, HOLMGREN and STENSIÖ 1936, DE BEER 1937, JOHNELS 1944).

The earlier authors mentioned here have, as a rule, only given a summary account of the morphology of the muco-cartilage. More detailed studies have been carried out, since reconstructions of the extension of the muco-cartilage in the skull have been made. As already pointed out in the introduction, marked differences in opinion have been expressed regarding the extent of the muco-cartilage. For instance, TRETJAKOFF (1929 a) considers the muco-cartilage to have but a limited extent, and the various muco-cartilaginous elements are often regarded as having no particularly close connection with each other. On the other hand, HOLMGREN and STENSIÖ (1936) interpret the greater part of the connective tissue complexes in the head as muco-cartilage. The opinions of other authors generally lie between these two extremes.

The most important muco-cartilaginous elements (fig. 3) are the ventro-lateral plate, the rostro-dorsal plate, the lateral mouth plates connecting these two formations, the subocular muco-cartilaginous elements running caudally from the lateral parts of the rostrodorsal plate, the subotic muco-cartilage parts, the ventro-medial longitudinal bar connected with the muco-cartilage axis

in the medial tentacle, the lateral and the medial velar skeleton, and the muco-cartilage discs situated laterally in the upper lip. In addition, certain minor muco-cartilaginous elements occur in connection with the branchial basket.

The biggest of these muco-cartilaginous complexes is the ventro-lateral plate situated ventrally to the cavities of the mouth and pharynx (SEWERTZOFF 1916—17, BALABAI 1935, HOLMGREN and STENSIÖ 1936, "Kiemenplatte" SCHNEIDER 1879, "Mund- Rachenhöhlenplatte" + "Schilddrüsenplatte" SCHAFFER 1896, "Ventral plate" GASKELL 1900, "Präbranchiale Platte" TRETJAKOFF 1929 a). The ventro-lateral plate has largely a superficial position. Ventrally it borders on the aponeurosis of the corium, from wich it is partly separated by a vascular plexus (STENSIÖ 1927, HOLMGREN and STENSIÖ 1936), otherwise lying medially to the parietal musculature. The visceral musculature, on the other hand, has on the wohle a medial position in relation to the ventro-lateral plate, although it is at times almost entirely surrounded by muco-cartilage. According to SCHAFFER (1896), the intermediate space between the ventral longitudinal bars of the branchial basket is completely filled with muco-cartilage, close to their point of fusion on a level with the fifth gill slit. However, this, no doubt, represents merely an intermediate stage in the development of the larva, in view of the fact that in younger specimens (up to 35 mm) the muco-cartilage extends further caudad. This extension will only take place in a superficial area, ventrally to the ventral longitudinal bars. In the particular specimen reproduced in fig. 3, not only this superficial layer of muco-cartilage is lacking, but also a part situated rostrad. Accordingly, the muco-cartilage does not fill up the most caudal region between the ventral longitudinal bars. Laterally, in this region, a contact is established between cartilage and muco-cartilage slightly rostrad to the forth branchial arch, a contact which is, moreover, broken for a short distance ventrally to the third as well as to the second branchial arch. From the ventral part of the first branchial arch, the free edge of the ventro-lateral plate runs rostro-dorsad and fuses with the subotic muco-cartilaginous portion. This edge thickens gradually rostrad and forms, ventrally to the point of fusion with the subotic portion of the muco-cartilage, a large pad of muco-cartilage (fig. 5). Medially, the pharyngeal musculature has been pushed aside so that the muco-cartilage comes into direct touch with the connective tissue situated under the epithelium in the cavity of the mouth. The connective tissue is at this point particularly well developed.

Cadually the subotic muco-cartilage portion connects with the first branchial arch, immediately before this arch in its turn joins the parachordals. From here this muco-cartilaginous mass stretches ventrally to the auditory capsule rostrad to the pedicle process, the lateral tip of which is surrounded by it. The semi-lunar lateral velar skeleton attaches with its caudo-dorsal end, to the rostral part of the muco-cartilage portion in the place where it forms the coalescence between the ventro-lateral plate and the subotic mass of muco-cartilage.

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In young specimens (32 mm or less) the subotic muco-cartilage masses are closely connected with the ventral side of the auditory capsules. However, that is not the case in older specimens. The musculus velohyoideus (TRETJAKOFF 1929 a) is partly fastened to the subotic muco-cartilage, which it penetrates deeply, sometimes completely piercing it (fig. 30).

The border of the ventro-lateral plate extends rostro-ventrally from the point of attachment of the lateral velar skeleton. Before proceeding rostrally into the edge of the lower lip to join its counterpart on the other side, the muco-cartilage in the ventro-lateral plate is medially connected with the ventro-lateral parts of the lateral mouth plates (fig. 4).

The lateral mouth plates (HOLMGREN and STENSIÖ 1936, "l'apophyse vestibulaire" DAMAS 1935) are ventro-medially united by a commissure which is separated from the muco-cartilage in the ventro-lateral plate by musculature, viz., the musculus depressor labii superioris and sublabialis (TRETJAKOFF 1929 a). Medially they are also combined with the muco-cartilage and connective tissue of the medial tentacle. Dorsally the lateral mouth plates are faintly curved mediad, where they fuse with the muco-cartilaginous parts ventrally and slightly caudally to the trabecular commissure. From here muco-cartilaginous parts extend, slightly caudad and, partly, rostrad round the trabecular commissure itself which, however, is left without a muco-cartilaginous coating on the ventral side. In this way, a ring of muco-cartilage is formed round the mouth opening ("Perioraler Bogen", BALABAI 1935). Corresponding to the conditions in the thickened edge of the ventro-lateral plate, ventrally to the pedicle, the muco-cartilage in the lateral mouth plates runs close to the epithelium of the cavity of the mouth, from which it is separated by strongly developed connective tissue (fig. 4).

The muco-cartilage in the medio-ventral tentacle passes caudally into the muco-cartilage in the ventro-medial longitudinal bar. This latter term is applied to the continuation caudad of the muco-cartilage in the dorsally projecting mucous membrane fold ventro-medially in the cavity of the mouth. The ventro-medial longitudinal bar extends caudally to the level of the first gill slit. In several places a connection is found between this structure and the ventro-lateral plate ventrally to it. This connection is more pronounced in young specimens. The muco-cartilage in these two formations is otherwise separated by musculature (musculus sublabialis and pharyngeus, TRETJAKOFF 1929 a).

The previously mentioned muco-cartilaginous masses situated in the region of the trabecular commissure are rostrally connected with the medio-caudal part of the rostro-dorsal plate (HOLMGREN and STENSIÖ 1936, "Dorsal plate", GASKELL 1900, "Cartilago dorsalis", SEWERTZOFF 1916—17, "Plaque prénasale", DAMAS 1935). This formation is the supporting element of the upper lip. The greater part of the muscles in the upper lip (musculus buccalis anterior, TRETJAKOFF 1929 a) attach to the ventral side of the rostro-dorsal plate. The ventral

surface of the rostro-dorsal plate is thus broken up into a number of processes and lamellae that surround the dorsal parts of the muscles. The dorsal surface which comes into contact with the connective tissue layer formed in the corium is, on the other hand, even.

Laterally, in the upper lip of older larvae there are two isolated muco-cartilaginous complexes which are, in younger larvae, directly connected with the rostro-dorsal plate as well as with the rostral part of the ventro-lateral plate. Later, these muco-cartilaginous bridges gradually grow thinner, finally completely disappearing and leaving the lateral muco-cartilaginous discs isolated.

Dorsally and caudally, the rostro-dorsal plate forms a depression where the nasal capsule is localized. Ventrally a contact surface between the cartilage in the nasal capsule and the surrounding muco-cartilage remains even in late larval stages. In earlier stages (e.g., 32 mm), however, the nasal capsule is practically surrounded by muco-cartilage on all sides exept dorsally.

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The two subocular muco-cartilaginous bars extend caudad from the lateral parts of the rostro-dorsal plate. Rostrally they have the appearance of vertical lamellae which, however, rapidly become narrower and continue, caudally, into dorso-ventrally somewhat flattened bars. Ventrally to the eye, the muco-cartilage of these formations unites without any distinct border with the connective tissue round the orbit which is thickened ventrally ("thickened bar of the orbital capsule", HOLMGREN 1943 a). This string of tissue connects caudally with the muco-cartilage surrounding the pedicle.

The rod-shaped, medial velar skeleton elements unite with the ventral surfaces of the trabeculae approximately on a level with the notochordal tip. Ventrally to this, the dorsal parts of the medial velar skeleton elements are connected with a muco-cartilaginous commissure (JOHNELS 1944). The two slightly arcuate rods diverge from each other ventrad.

In the branchial region, there are, further, some scattered formations of muco-cartilage. The branchial arches describe a rostrally convex curve, dorsally to the epitrematic longitudinal bar, as well as ventrally to the hypotrematic one. On each branchial arch these particular places are rostrally covered by a muco-cartilaginous plate.

The above description differs in several respects from earlier ones. As regards the caudal parts of the ventrolateral plate, the subotic muco-cartilage portions and the part round the nasal capsule, it has been pointed out above that there are differences between various stages of development. However, such a simple observation cannot be generally applied as an explanation of diverging opinions.

SEWERTZOFF (1916—17), TRETJAKOFF (1929 a), BALABAI (1935) and DAMAS (1935) are of the opinion that the muco-cartilage in the upper lip only forms a very restricted pre-nasal plate. In this case the explanation of the difference

in opinion may, perhaps, lie in the different histological structures of the central and peripheral parts of the rostro-dorsal plate. In the center the histological structure resembles to a great extent that observed in the ventro-lateral plate, with relatively densely situated cells and regularly orientated cellular processes. However, peripherally the muco-cartilage of the rostro-dorsal plate is characterized by gradually sparser cellular elements which, in addition, do not have a regular orientation. The cells themselves and their branches seem to be principally of the same type throughout. As already demonstrated by GASKELL (1900) by means of thionin, which stains the intercellular substance of the muco-cartilage metachromatically, also the intercellular substance everywhere in this region seems to show identical characteristics. The histological differences which exist between the various parts of the rostro-dorsal plate are, accordingly, only to be interpreted as differences in degree. In the present author's opinion, therefore, the limited extension ascribed to the muco-cartilage by the forementioned investigators seems to a certain extent arbitrary.

SEWERTZOFF (1916—17) and TRETJAKOFF (1929 a), in their descriptions, also omit to mention the muco-cartilaginous masses in the region of the trabecular commissure. The result is that the lateral mouth plates are not considered to fuse with each other, nor with the rostro-dorsal plate. On the other hand, DAMAS (1935) draws attention to the contact existing between the lateral mouth plates and the rostro-dorsal plate, but does not mention the muco-cartilage round the trabecular commissure. This latter element is reproduced by BALABAI (1935) who, nevertheless, in his description omits to note a connection between the dorsal muco-cartilaginous parts and the lateral mouth plates. However, he does refer to what he calls a "perioraler Bogen". The reason for these divergent statements in the literature may, conceivably, be variations in the occurrence of muco-cartilage. On the other hand, the conditions described in this paper were without exception in the present material.

DAMAS has, in his comprehensive embryological work published in 1944, expressed the opinion that such divergencies may be due to the fact that the larvae examined have been at different stages of development. This explanation will—as mentioned—probably hold good at least in part.

Earlier, conditions connected with the histogenesis of the muco-cartilage have been discussed. The long time elapsing before the mesenchyma designed for muco-cartilage loses its embryonic character is especially mentioned. The fact that muco-cartilage and other kinds of connective tissue often originate from a coherent mesenchyma which is a primordium of different types of connective tissue greatly adds to the difficulty in rendering a definite distinction between the various types of connective tissue in the head of younger larvae.

HOLMGREN has, after studies of early larval stages ("ganz jungen Petromyzonlarven"), arrived at the conclusion that the greater part of the connective

tissue of the head should be regarded as muco-cartilage (cf. HOLMGREN and STENSIÖ 1936, figs. 227 and 228). The connective tissue fibres surrounding the muscles are, however, in post-embryonic stages of an unmistakable collagenous nature. Still, after staining with Bismarck brown and with several so-called mucous dyes, it appears conceivable that an intercellular substance, resembling that of muco-cartilage, should form part of these connective tissue complexes. The use of other dyes, such as those with a metachromatic stain, nevertheless contradicts this assumption. No metachromatic staining can be produced in these places. Accordingly, the elements characteristic of muco-cartilage do not develop within, or in the proximity of, the perimysia, provided they are not directly connected with the surface of one of the muco-cartilaginous complexes referred to.

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Although the muco-cartilage—in full-grown larvae—can be relatively easily distinguished from the connective tissue surrounding the musculature, this may in other parts involve considerable difficulties. This applies to the three bars stretching caudad from the rostro-dorsal plate, as described by GASKELL (1900) and homologized by him with the pectoral cornua and the dorsal, caudal part of the cephalic shield of Cephalaspids. In the Ammocoetes larva, these formations (fig. 3 *c.t.*) are situated in the dorsal myoseptum and ventrally to the musculus supraocularis (TRETJAKOFF 1926 a). The medial, dorsal bar is attached at the dorso-caudal part of the nasal capsule and extends caudad from there. The bars lying ventrally to the supraocular muscles appear best developed laterally to the auditory capsules with which they are broadly connected. Caudally to the auditory capsule, these formations fuse with fibrous connective tissue of a normal type. Rostrally they run laterally to the eyes, also covering them, and attach to, or in the proximity of, the lateral side of the so-called subocular muco-cartilaginous process. These formations, at all stages of development, only form lamellae.

The muco-cartilaginous character of these formations seems doubtful. It is true that metachromatic staining gives the impression that a matrix, such as in the muco-cartilage, should have formed, while the cellular elements are, to all appearances, lacking. Collagenous fibres have developed in connection with the adjacent, parietal musculature.

Between the muco-cartilaginous arch which is formed by the ventro-lateral plate and the subotic muco-cartilage portion, and the cartilaginous loop running rostrally to the first gill slit, loose connective tissue extends. This tissue contains also an abundance of adipose cells. SCHNEIDER, as early as in 1879, described the occurrence of adipose cells in Ammocoetes. GASKELL (1900) pointed out that a layer of these cells, i.e. a so-called fat layer, covered the spaces between the branchial arches in the whole branchial basket. He interpreted this layer as the remnant of a degenerated layer of muco-cartilage.

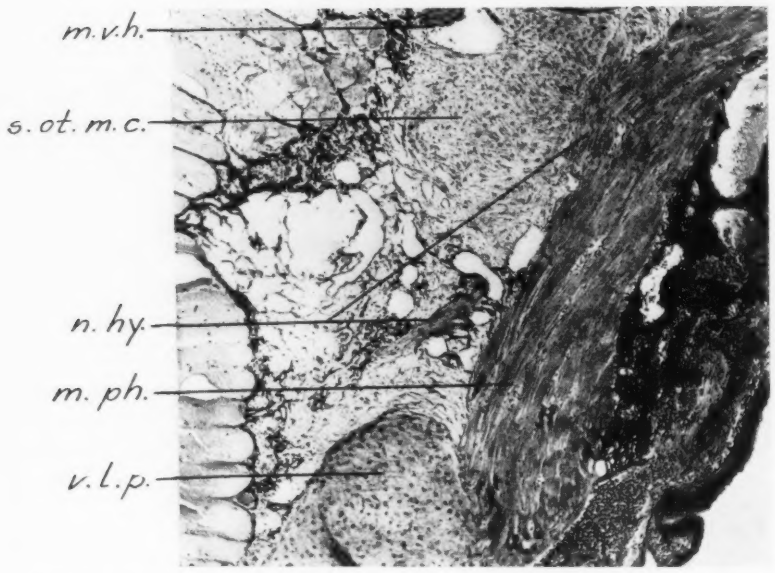

Fig. 5. Larva, 120 mm. Transversal section through the left body wall caudally to the point of fusion between the subotic muco-cartilage portion and the ventro-lateral plate. 80 ×.

Caudally, the muco-cartilage transforms, with a short transitional zone, into this connective tissue. The matrix, characteristic of the muco-cartilage, gradually disappears in this area, as manifested by the loss of stainability. The cellular elements typical of muco-cartilage become rare and an increasing number of adipose cells, and transitional cell types, is seen between them. This transitional zone remains till the metamorphosis. Caudally to this part, where the muco-cartilaginous character is still evident, the ramus hyoideus of the facial nerve (TRETJAKOFF 1927 a) runs from the medial side of the muco-cartilage laterad (fig. 5).

3. THE EMBRYONIC DEVELOPMENT.

Ever since A. MÜLLER, in 1856, showed that Ammocoetes only represented a larval form that would later, by methamorphosis, change into a Petromyzon, a great number of authors have dealt with problems connected with the embryonic development of this animal. However, but a few have studied the formation and development of the skull (SCHULZE 1856, CALBERLA 1877, PARKER 1883, DOHRN 1884, SHIPLEY 1886—87, KUPFFER 1894, 1895, SEWERTZOFF 1897, 1913, 1916—17, KOLZOFF 1899, 1901, GOETTE 1901, SCHALK 1913, HATTA 1914—15, and DAMAS 1944).

The first cartilaginous elements formed in the skull of Petromyzon are the

branchial arches which develop from the fore-part backwards. They appear as small rods consisting each of a single row of procartilaginous cells. They develop caudally to the appertaining gill slit. Later, the ventral ends fuse with the ventral longitudinal bar, while the dorsal ends grow dorsad towards the notochord. Somewhat later the other longitudinal bars develop. The epi- and hypotrematic longitudinal bars arise as rostral branches from each branchial arch. Only the primordia of the hypotrematic bar fuse with the nearest anterior arches. The subchordal longitudinal bar forms as a rostral, as well as a caudal, branch from the dorsal parts of each arch. These branches then join each other. The subchordal longitudinal bar in the rostral half connects with the ventro-lateral side of the notochord only at fairly late stages. It is originally free from the notochord. The first branchial arch does not fuse with the subchordal longitudinal bar. Instead it will unite, dorsally, with the parachordal, which develops in relation to the notochord on a slightly higher level than the subchordal longitudinal bar.

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As pointed out by BALFOUR (1881), the branchial arches in Petromyzon develop in a superficial position. They form from the very beginning laterally to the appertaining vessels and nerves. DOHRN (1884) attempted to prove that this should indicate an adaptation to certain functional conditions, manifested secondarily during the ontogenetic development. However, this opinion has been repudiated on the basis of embryonic facts presented by GOETTE (1901), and DAMAS (1944), among others. According to DAMAS, also the muco-cartilaginous components in the skull develop in the same superficial cellular layer that gives rise, caudally, to the branchial arches, etc. DAMAS further demonstrated that an arch develops also in the hyoid segment. This arch, however, never reaches further than to a feebly developed procartilaginous stage. Later, this tissue changes into mesenchyma which produces the muco-cartilage of the caudo-dorsal edge of the ventro-lateral plate.

In the cranial base the trabecles develop as the cartilaginous elements first formed. To begin with, they lie parachordally, in the literal sense of the term. This caused SEWERTZOFF (1916—17), and others, to interpret them as parachordal elements (cf. page 256). The trabecles later grow rostrad. PARKER (1883) and DAMAS (1944) have described stages where they are connected rostrally by a blastematic band on the border to procartilage. This tissue will, later, give rise to the trabecular commissure. Caudally, the trabecular primordium merges into the tissue forming the anterior primordium of the parachordal cartilage. The posterior primordium of the same cartilage develops caudally to the auditory capsule. SCHALK (1913) detected a boundary between the cartilage forming the first branchial arch and the parachordal cartilage, as was also observed by DAMAS (1944). The anterior portion of the future parachordal is connected with the caudal part of the trabecle. The two parachordal primordia change into cartilage separately, and then grow towards each

other along the notochord medially to the auditory capsule. On a level with the caudal limit of the trabecle, the laterally directed pedicle process appears as an independent primordium (DAMAS 1944).

Simultaneously with the union of the two primordia of the parachordals, cartilage appears in the nasal and auditory capsules. The cartilaginous element in the nasal capsule is originally paired (DAMAS 1944). This was presumed, as early as in 1916—17, by SEWERTZOFF.

As regards the opinions concerning the origin of the various skeletal parts, an influence can be traced at an early date, from the valuable results arrived at by PLATT (1893, 1894 a, 1894 b, 1898) on the formation of the cranium in Amphibia. KUPFFER (1894, 1895), accordingly, attributed the development of the branchial skeleton to ectomesodermal tissue ("neurodermis" or "branchiodermis"). Broadly speaking, the same opinion was held by KOLZOFF (1901), SCHALK (1913) and DAMAS (1944). Only HATTA (1914—15) contended that no skeletal material is derived from ectoderm.

DAMAS (1944) devoted much attention to the formation and development of the ectomesoderm. He states: "Il dérive de la crête neurale, des placodes, des ébauches nasale et buccale. Il se répartit en deux régions réunies autour du cerveau antérieur. Le mésectoderme dorsal gaine complètement le névraxe et fournit ses enveloppes. Le mésectoderme ventral n'existe qu'autour de la bouche et du pharynx. Il s'y développe en deux couches, une superficielle sous-épidermique et une profonde, collée contre le diverticule buccal et la paroi digestive. Ce mésectoderme ventral donne naissance à presque tout le squelette cartilagineux, a l'entièreté du squelette membraneux et aux gaines des vaisseaux sanguines." Only the parachordals and the auditory capsules were assumed to have a purely mesodermal origin.

The opinions advanced by DAMAS agree, in several respects, with those set down earlier by KOLZOFF (1901). As to trabecles and parachordals, however, KOLZOFF maintained that they are formed in the sclerotome of the first and second segments (enumerated according to WIJHE 1882). Still, he suggested that the growth rostrad of the trabecles and the development of the trabecular commissure might take place at the expense of ectomesodermal cellular elements. Caudally the growth of the cranial base was stated to take place in the sclerotomes in that region. SCHALK (1913) was of the opinion that the trabecles are in their entire extent merely somitic. On the other hand, VEIT (1940) emphatically denies the existence of prootic mesomeres and, consequently, attributes to the ectomesoderm a dominating rôle in the formation of the anterior skeletal parts of the head.

According to DAMAS (1944), the first segment (i.e. the premandibular) partly gives rise to musculature (oculumotorius innervated), and partly also perhaps to mesenchyma. This mesenchyma was supposed, nevertheless, to have no significance with regard to the formation of skeleton. However, he asserted,

in accordance with KOLZOFF, that the first segment should be interpreted as a scleromyotome.

As regards the second (the mandibular) segment, DAMAS maintained that no separation into a scleromyotome and a lateral plate takes place. He mentioned concerning one stage (60 segments) a formation of mesenchyma in the dorsal part of the segment which was, however, to play a part only in the formation of musculature. In a drawing in his publication of 1944 (fig. 63) the lettering "scl. s. 2." apparently indicates that DAMAS, at some time during his work, assumed that a sclerotome had actually developed in this segment.

In the third and the fourth, i.e. in the hyoid segment, and in the first postotic segment, on the other hand, sclerotomes are stated to have developed. The mesenchyma deriving from these sclerotomes is assumed to form the primordia of parachordals and auditory capsules.

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In the region of the head corresponding to the first two segments, the skeletal material in the cranial base developed, according to DAMAS, from an ectomesodermal formation which he terms "le bande mésectodermique parabuccale". Moreover, from this parabuccal cellular band the medial velar skeleton derives. The part which DAMAS regards as the primordium of the trabecle lies laterally to the paired dorsal aorta. At the stages when the arteria mandibularis is developed, this artery runs laterally to the trabecular primordium and joins the aorta dorsalis dorsally.

The main purpose of the present investigations regarding the embryonic development of Petromyzon was originally to check earlier observations concerning the skeleton. As to the development of muco-cartilage, the branchial basket, parachordals, nasal and auditory capsules, etc., the opinions of KOLZOFF (1901) and DAMAS (1944), who are, on the whole, in agreement on this subject can be confirmed here. Particular attention has been paid to the formation of the trabecles on account of the exceedingly contradictory statements concerning them.

It seems unlikely that KOLZOFF could have interpreted the trabecular primordium described by DAMAS as sclerotomes. KOLZOFF dealt chiefly with early embryonic stages where the position of the parabuccal cellular band renders such an interpretation impossible. The caudal end of the parabuccal cell band is at these stages without any contact with the sclerotomes in the third segment, as is evident, inter alia, from the drawings published by DAMAS. Also, rostrally, the position is such that the sclerotomes that may exist—even in view of the invagination of the mandibular segment—should lie dorsally to the parabuccal cellular band. Accordingly, it seems more probable that DAMAS and KOLZOFF not only described different origins for one and the same trabecular primordium, but also examined two entirely different trabecle primordia.

As may be seen from the following description of certain stages in the present material, the author has discovered a special trabecular primordium dorsally to the parabuccal cell band.

a. *Stage 1.* (317 hours, fig. 6.)

This stage is characterized, inter alia, by the fact that the arteria mandibularis (fig. 7) has begun to disappear. Rostrally, the paired dorsal aorta is divided on either side into two branches, viz., a dorsal and a ventro-lateral one (cf.

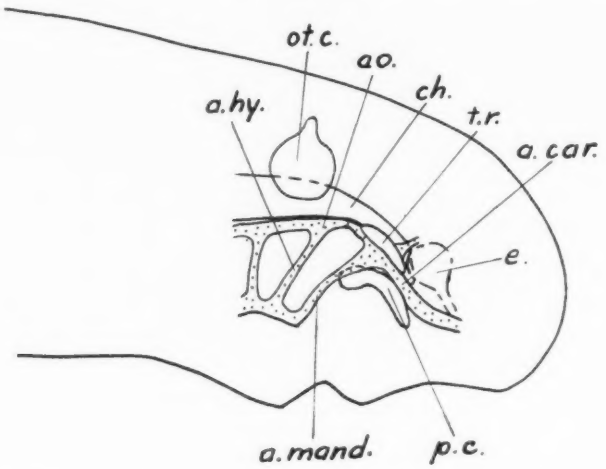

Fig. 6. Embryo, 317 hours. Reconstruction of head. Lateral view. 100 ×.

CLAYDON 1938). From the latter, the part of the aorta dorsalis running medially to the trabecle is formed (the arteria carotis, HATTA 1922—23).

Ventro-laterally to the aorta dorsalis the parabuccal cell band is seen. In its caudal part the tissue is well delimited, but becomes more diffuse rostrad. Laterally and dorsally to the caudal part of the parabuccal cell band, the arteria mandibularis runs—as demonstrated by DAMAS—and joins the paired aorta dorsalis (fig. 7). The latter vessel runs rostro-ventrad dorso-medially to the cell band.

Dorsally to the parabuccal cell band and laterally to the aorta dorsalis lies the trabecular primordium as a mesenchymal accumulation (fig. 7). The position corresponds well to the lettering "scl. s. 2." made by DAMAS (1944, fig. 63). Caudally, the mesenchyma is comparatively easily discerned, but even in this primordium the rostral part is diffuse. Caudally to this mesenchymal pad, there is a similar, though less dense, mesenchymatic area, representing the sclerotome of the hyoid segment.

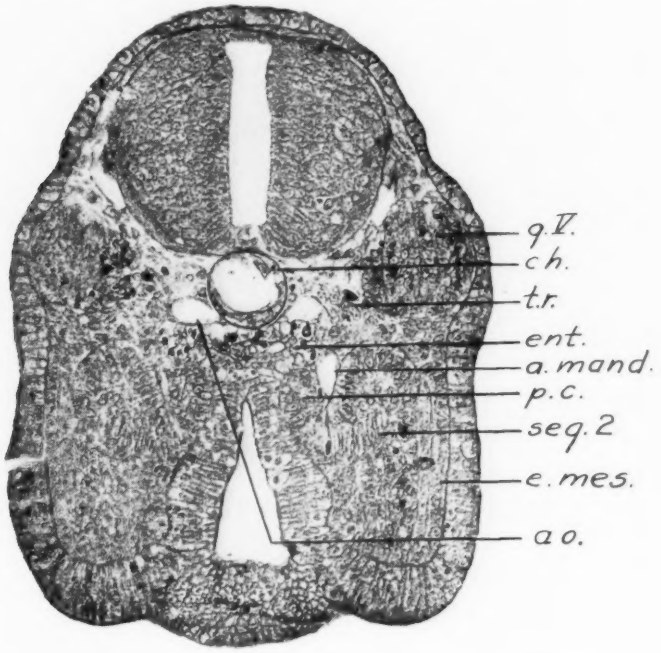

Fig. 7. Embryo, 317 hours. Transversal section through the mandibular segment. 220 ×.

Ventrally to the caudal part of this trabecular primordium, the arteria mandibularis is connected with the aorta dorsalis. The latter vessel turns ventrad to the rostral part of the primordium, after having sent forth its dorsal branch somewhat laterally, and runs between the parabuccal cell band and the trabecular primordium.

b. *Stage 2.* (355 hours, fig 8.)

At this stage the arteria mandibularis has disappeared. The trabecular primordium has, on the whole, the same form as in the preceding stage, though slightly prolonged both rostrad and caudad. The mesenchyma has simultaneously become somewhat more compact.

The parabuccal cell band has changed considerably in shape as well as in size. The caudal part has been enlarged and extends caudo-ventrad from the rest to wich it forms practically a right angle. The dorso-rostral part has maintained its position unchanged from the preceding stage. It is situated laterally to the dorsal part of the invaginated, ectodermal stomodeum. The caudal part lies closer to the medial plane between the ectoderm of the stomo-

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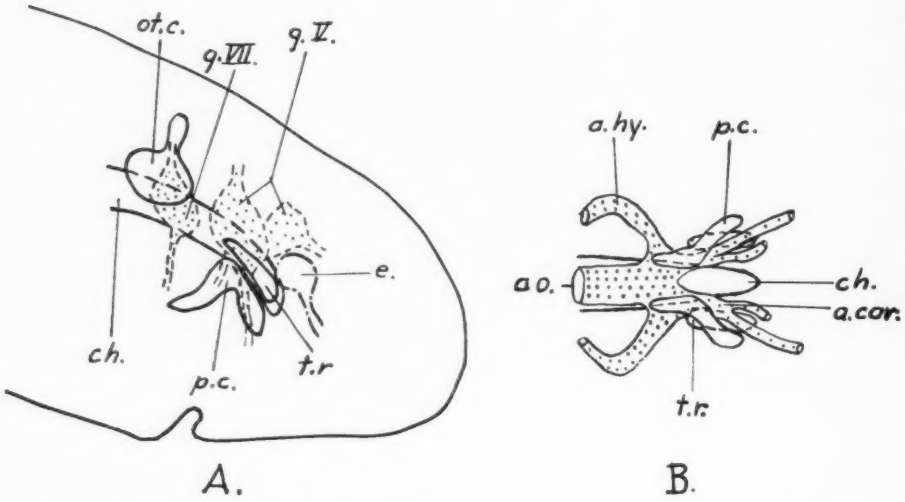

Fig. 8. Embryo, 355 hours. Reconstruction of head. A. Lateral view, B. Ventral view. 100 ×.

deal primordium and the entoderm of the anterior intestine. The rostral prolongation of the paired aorta dorsalis runs between the trabecular primordium and the parabuccal cell band. The mesenchyma caudally to the trabecular primordium is still diffuse.

c. *Stage 3.* (365 hours, fig 9.)

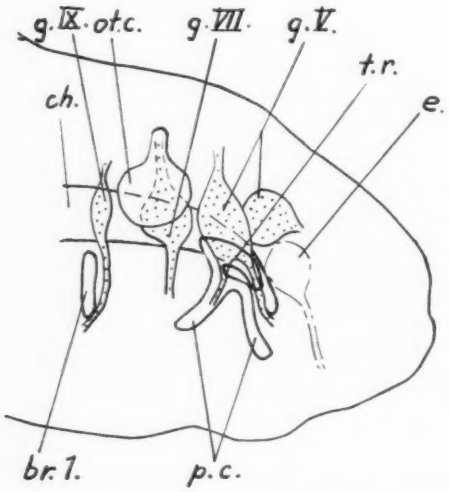

Fig. 9. Embryo, 365 hours. Reconstruction of head. Lateral view. 100 ×.

At this stage, which follows fairly close on the previous one, the first branchial arch has developed as a small rod of procartilage.

The trabecular primordium has grown slightly caudad. Ventrally a connection has been established with the parabuccal cell band. In the dorso-rostral part of the latter structure, a distinct reduction has taken place, simultaneously with an enlargement of the stomodeal invagination. This part has, in addition, lost its sharp delimitation. On the other hand, the caudo-ventral part has developed in comparison with the preceding stage. It has,

broadly speaking, the position taken by the medial velar skeleton in the velum at later stages, between the ectoderm of the stomodeal invagination and the entoderm of the anterior intestine.

d. *Stage 4.* (410 hours, fig. 10.)

The rostro-dorsal part of the parabuccal cell band has entirely disappeared, while the other primordia have considerably developed. The trabecular primordium is now, partly, a blastema, on the verge of becoming procartilage,

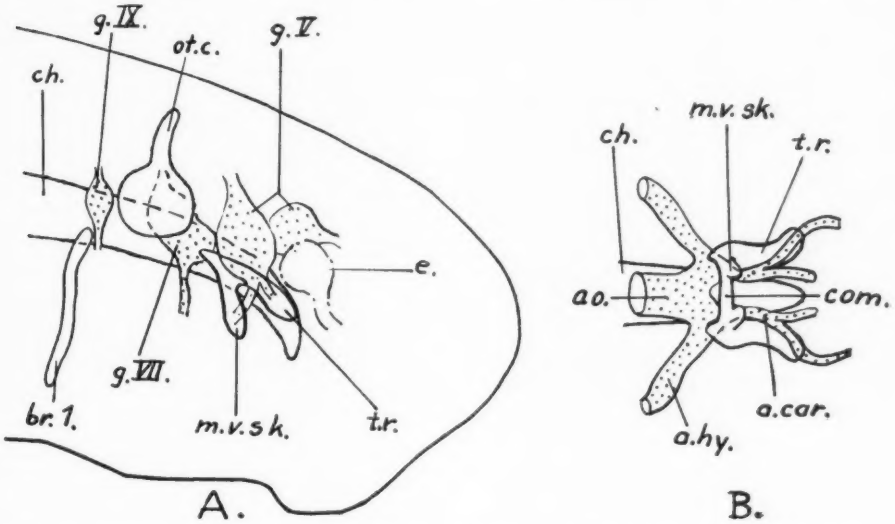

Fig. 10. Embryo, 410 hours. Reconstruction of head. A. Lateral view, B. Ventral view. 100 ×.

which has increased in extent, rostrally as well as caudally, where it connects with the notochord and comprises the anterior primordium of the parachordal cartilage. Also the medial velar skeleton (fig. 11) is a markedly compact blastema which, in connection with the development of the velar primordium, has obtained a rostro-ventral direction. A transversal commissure has formed between the dorsal ends of the velar skeletons, extending ventrally to the notochord, between it and the ventrally situated intestine (fig. 11). Dorsally to this commissure and ventro-laterally to the notochord, the paired dorsal aorta runs.

The rostro-dorsal part of the parabuccal cell band disappears very rapidly. It is, therefore, difficult to follow its exact course. The ectomesodermal material, however, probably spreads in the proximity of its original localization, simultaneously with the enlargement of the stomodeal invagination. It does not seem unlikely that the trabecular primordium in this connection obtains an

additional supply of cells. However, no signs of such a process have been observed.

This stage approximately corresponds to the specimen reproduced in the reconstruction No. 14 by DAMAS (1944).

The changes following next on the last described stage are comparatively uneventful as regards the development of the skeleton. The trabecles grow rostrad, and, at the same time, the so-called upper lip takes shape. The contact surface between the stomodeal invagination and the anterior intestine is per-

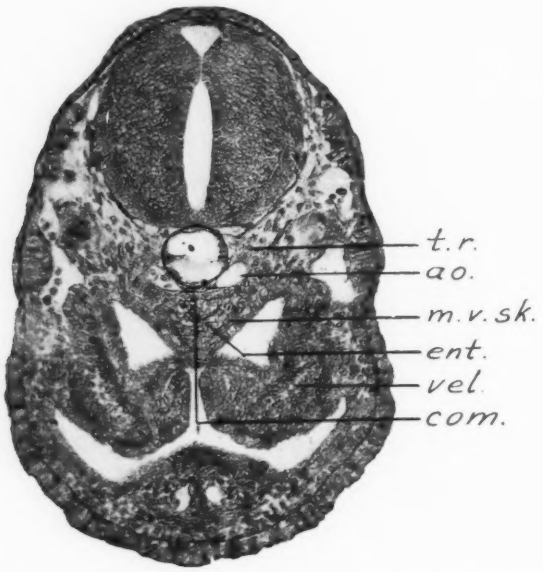

Fig. 11. Embryo, 410 hours. Transversal section on a level with the medial velar skeleton and the commissure. 140 ×.

forated medially close on the last mentioned stage. From now the velar apparatus assumes a shape suitable to its function (cf. DAMAS 1944). The ventral longitudinal bar is first formed, then the other bars, as previously described.

e. *Stage 5.* (618 hours, fig. 12.)

The trabecles have grown considerably in length and have become partly cartilaginous. Rostrally they both terminate in a small mesenchymal pad. At the point of attachment of the medial velar skeleton and the forementioned commissure, the cartilage of the trabecle has projected ventrad (fig. 13 b). Laterally a dense mesenchymal mass is connected with this part of the trabecle. This portion of mesenchyma represents the first primordium of the pedicle

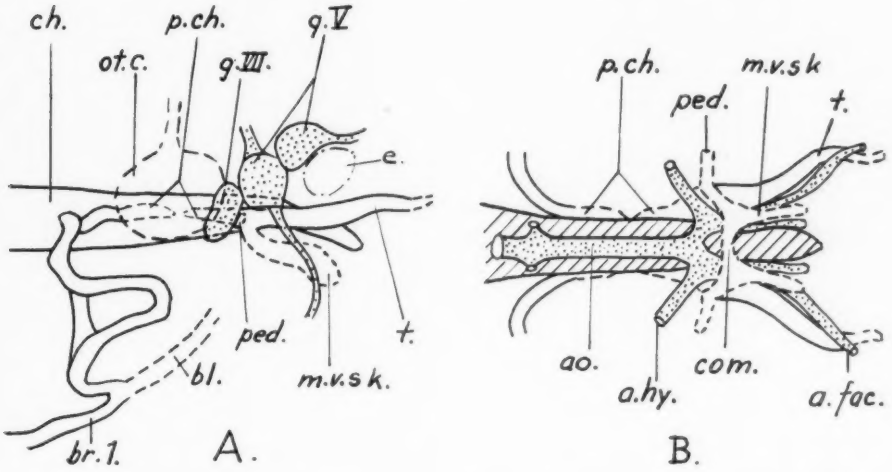

Fig. 12. Embryo, 618 hours. Reconstruction of head. A. Lateral view, B. Ventral view. 100 ×.

(fig. 13 a). Medially to this primordium the cartilage runs close to the notochord, and joins the anterior primordium of the parachordal cartilage. Caudally, this primordium consists of mesenchyma which ends in a tip medially to the auditory capsule. Caudally to this primordium, the posterior mesenchymal primordium of the parachordal cartilage runs along the dorso-lateral side of the notochord. Thus, the two primordia have not as yet fused. Caudo-laterad the caudal primordium joins the cartilage of the first branchial arch.

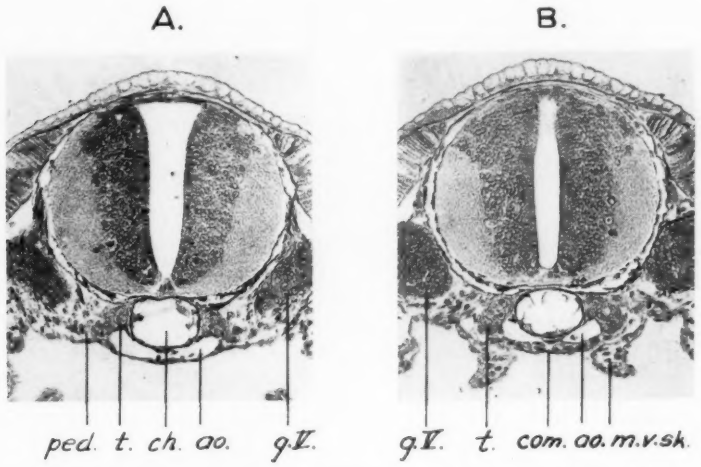

Fig. 13. Embryo, 618 hours. Transversal sections. A. on a level with the pedicles, B. on a level with the caudal part of velum. 140 ×.

The branchial arches have developed considerably. The subchordal, epitrematic and hypotrematic longitudinal bars are in the act of growing, while the ventral bar is already completely developed. At the point where this latter bar fuses with the first branchial arch, a rostrally convex curve is formed, characterized by a particularly pronounced cartilage formation. From this cartilaginous part a mesenchymal band, which is at first easily distinguished by a marked accumulation of cells, issues rostrad. However, it gradually becomes more similar to the surrounding mesenchyma in a dorso-rostral direction, finally disappearing.

f. *Stage 6.* (8 mm, fig. 14.)

As mentioned earlier, PARKER (1883) as well as DAMAS (1944) have described stages where the trabecles are rostrally united by a band of not yet cartilaginous tissue. This, no doubt, represents a somewhat later stage.

The trabecles join rostrally by means of a cartilaginous bar which, on one side, has not yet reached the trabecular tip. This is probably due to a separate formation of cartilage in the trabecular commissure. Thus, there is, apparently, no growth of the trabecles rostrad that would finally result in the formation of a trabecular commissure, as assumed by SEWERTZOFF

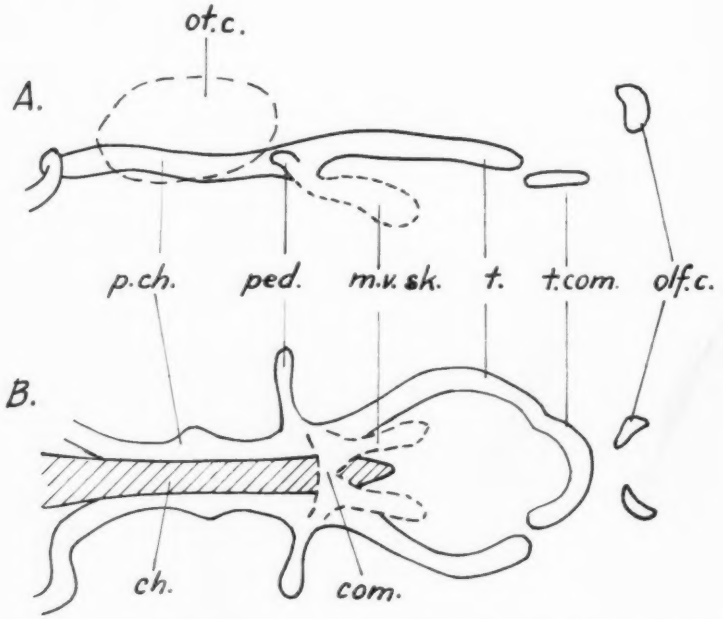

Fig. 14. Young larva, 8 mm. Reconstruction of skull. A. Lateral view, B. Ventral view. 80 ×.

(1916—17). On the other hand, the trabecles and the rostral part of the parachordals caudally develop in one piece.

From the cartilage in the trabecle a cartilaginous projection issues ventrad towards the strongly compact mesenchyma in the medial velar skeleton and the transversally proceeding commissure (fig. 15). Laterally to this, the pedicle has become entirely cartilaginous, while being medially connected with the above-mentioned blastematic formations by means of a mesenchymal strip of tissue ventrally to the trabecle. The two primordia of the parachordal cartilage have united and changed into cartilage. Medially to the auditory capsule, around which no cartilage has as yet appeared, a lateral blunt process of the parachordal cartilage is seen. This represents the first primordium of a future connection with the cartilaginous auditory capsule.

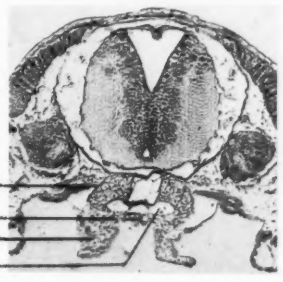

Fig. 15. Young larva, 8 mm. Transversal section on a level with the caudal part of the velum. 90 ×.

Rostrally a small piece of cartilage is situated on either side of the nasal vesicle. As demonstrated earlier by DAMAS (1944), the cartilage formed in the nasal capsule is, accordingly, primarily binary.

As is evident from the above it is not, in the present author's view, probable that the parabuccal cellular band should represent the primordium of the trabecles. This formation is situated ventrally to the rostral prolongation of the aorta dorsalis. It is from this part of the aorta that the artery develops which runs medially to the trabecle and rostrally passes in a curve, venrally to this cartilage, into the arteria facialis (HATTA 1922—23). On the other hand, such a relationship to this vessel is manifested by the trabecular primordium described by the present author. As already shown by DAMAS (1944), the arteria mandibularis, when present, runs in a curve, laterally and dorsally to the premandibular cell band, before joining the aorta dorsalis. Dorsally to the arteria mandibularis lies the trabecular primordium described here. As maintained by DAMAS, the parabuccal cell band is without doubt ectomesodermal. On the other hand, it is difficult to determine the origin of the trabecular primordium.

It is necessary to emphasize here, before entering into a discussion of this problem, that it can be conclusively settled only by means of experimental investigations. As regards Petromyzon, such investigations have been made only in connection with the construction of the so-called "Anlageplan" (WEISSENBERG 1926, 1934, 1936). DAMAS (1944) has, apparently, made extensive attempts to apply vital staining methods in his investigations. However, he did not obtain the desired results, and discusses the reasons in detail. The present

author has, in the course of this work, not had the opportunity to make use of such a technique. This notwithstanding, indications, though indecisive, have been found for a discussion of the above-mentioned problem.

The trabecular primordium described in this paper is probably identical with that observed by KOLZOFF (1901). He, of course, considered that it was the parachordal cartilage that developed in the sclerotome of the mandibular segment, but this is, in this particular connection, of minor importance. The essential fact is that the primordia, according to KOLZOFF, are somitic. As previously mentioned, also DAMAS (1944) noticed a mesenchymal formation in the dorsal part of the first two segments. It seems likely that this mesenchyma gave rise to the trabecular primordia, shortly after its formation, although this cannot be objectively established by the methods employed. Obviously the parabuccal ectomesoderm in its primary position cannot be considered to be a trabecular primordium, nor does a breaking-down of this originally well defined structure set in until the trabecular primordium is relatively clearly discernible. Otherwise the ectomesoderm is fairly sparse in the earlier stages, when the trabecular primordia have already become visible. However, this ectomesoderm can, of course, be conceived to take part in the formation of the trabecular primordium, but at the actual formation of the trabecle no direct reasons for such a conclusion have been observed. As pointed out by KOLZOFF, this is on the other hand probable more rostrally. Here, in fact, at later stages the trabecular commissure changes into cartilage relatively independently, which may be interpreted as indicating the correctness of this assumption.

Practically all investigators agree in the view that the sclerotome of the third segment provides material for the parachordal cartilage. The trabecle passes caudad into the anterior part of the parachordal primordium without any visible delimitation. The parachordal cartilage develops simply by a growth caudad of the former. Further, the mesenchyma in the sclerotome of the third segment does not seem to have any greater extent nor to be more easily observed than that of the segment in front. Instead, the formation of blastematic tissue and of cartilage is retarded at this point. The intimate contact between the cells in the sclerotome of the third segment and the trabecular primordium in front of it is, probably, due to a deviation rostrad of the dorsal parts of this segment through the development of the auditory capsule. The distance to the fourth and fifth segments, from which the material for the rest of the parachordal cartilage is obtained, becomes proportionately the greater.

No histological differences in the mesenchyma of the trabecular primordium and in the anterior primordium of the parachordal cartilage have been ascertainable. On the other hand, the difference between this mesenchyma and the adjacent ectomesoderm is also difficult to discern, at any rate at later stages (cf. DAMAS 1944). However, it seems, in the opinion of the present author,

probable that the trabecular primordium originates from the sclerotomes of the first and second segments.

The medial velar skeleton and the transversal commissure, no doubt, develop out of ectomesoderm, the former, at least, from the caudal parts of the parabuccal cell band. Also the pedicle seems to the author to be of ectomesodermal origin, as previously pointed out by DAMAS (1944).

IV. THE METAMORPHOSIS OF THE SKELETON OF THE HEAD.

The present account of the metamorphosis comprises a histological orientation, a description of 14 developmental stages and a summary of the skeletal transformation. Since the eye can be supposed to increase in size fairly continuously during metamorphosis, the diameter of this organ has been measured for each stage as an approximate sign of progress. This may, of course, involve individual variations that often reverse the order but, on the whole, such measurements may serve as a guide in the forementioned respect.

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1. THE METAMORPHOSIS FROM A HISTOLOGICAL POINT OF VIEW.

a. *The transformation of muco-cartilage into cartilage.*

SCHNEIDER, as early as 1879, suggested that muco-cartilage, in the course of metamorphosis, changes into cartilage. Some details concerning this process have been communicated by KAENSCHE (1890) and BUJOR (1890—92).

The first real histological observations of the transformation of muco-cartilage into cartilage were made by SCHAFFER (1896, 1897, 1901) and by STUDNIČKA (1897, 1898 a, b). SCHAFFER states that, before the formation into cartilage, the muco-cartilaginous cells differentiate and undergo divisions. During the later phases of the formation of cartilage, cells appear in which the nuclei stain better than cartilage and muco-cartilage cells. According to SCHAFFER, only cartilage with a poorly developed intercellular substance originates from muco-cartilage. Cartilage of this type will be found for example in the center of the rostral cartilaginous elements. The matrix of the peripheral cartilage is better developed and believed to be derived from the perichondrium. SCHAFFER is of the opinion that cartilage-forming cellular elements migrate into the areas of cartilage formation, but he omits to state from where they originate. However, he mentions that, without an access to stages from the metamorphosis, he has not been able to follow the formation of the cartilage in all its details. It is obvious (cf. p. 237) that the styliform cartilage, the principal subject of SCHAFFER's study, offers particular difficulties because of

the appearance of wandering cells. According to STUDNIČKA muco-cartilaginous cells can be directly transformed into cartilaginous cells.

TRETJAKOFF (1927 c, 1929 a) and DE BEER (1937), on the other hand, maintain that no cartilage arises from cells belonging to muco-cartilage. Their statements are, however, not accompanied by any histological accounts of the genesis of the cartilage and, as far as DE BEER is concerned, it is obvious that, in this particular respect, he has partly misinterpreted other authors, e.g., BALABAI (1935).

The latest contribution to our knowledge has been made by DAMAS (1935) who had at his disposal a more comprehensive material. He writes regarding the muco-cartilaginous elements: "Dès le début de la métamorphose, on observe, à la place du tissu élastique si particulier qui les composaient, une structure très voisine du tissu conjonctif ordinaire." The intercellular substance has lost in stainability. "Les élastoblastes" have changed into ordinary connective tissue cells. The elastic fibres have disappeared and fibres "tout à fait semblables aux fibres conjonctives ordinaires" have been substituted for them, while, at the same time, the number of cells has considerably increased. Simultaneously, the tissue has gained in volume. These observations refer to specimens that disclose "le moindre symptôme de transformation". Damas adds: "Elles doivent donc s'effectuer très brutalement et nous ne pouvons que décrire les résultats de cette première altération." DAMAS' conception of the elastic nature of the muco-cartilaginous cells has been discussed in the chapter dealing with the histology of the muco-cartilage (cf. p. 145).

From the above it is evident that the earlier stages of the transformation of the muco-cartilage into cartilage are but poorly known, owing, probably, to the fact that they can only be studied in specimens which do not reveal any outward signs of a commencing metamorphosis. In the course of the present investigation, preparations of a number of big larvae have been made, among which early stages of metamorphosis have been found. The changes are not synchronous in different parts of the muco-cartilage. This is, probably, at least in part due to the fact that the processes are far from being of the same nature everywhere in the muco-cartilage. These matters will be discussed later. Here an account will be given of the formation of cartilage from muco-cartilage regarded from a strictly histological point of view. For this purpose the process in the ventro-medial longitudinal bar has been chosen, since attention has, to some extent, to be paid to the changes in the tissues that surround the muco-cartilage. The ventro-medial bar offers fairly uncomplicated conditions in this respect. It has long been known that the so-called piston cartilage in the full-grown animal originates in the muco-cartilage in the ventro-medial bar.

The ventro-medial longitudinal bar in the larva of Petromyzon is dorsally and laterally enveloped by connective tissue. This constitutes part of the

collagenous layer below the mucous membrane of the cavity of the mouth. In this connective tissue a number of blood vessels will be found, in contrast with the muco-cartilage where such vessels are absent. The whole structure projects into the cavity of the mouth. Ventrad the muco-cartilage in the ventro-medial longitudinal bar is delimited from that of the ventro-lateral plate by the musculus pharyngeus and in the rostral parts also by the bundles of the

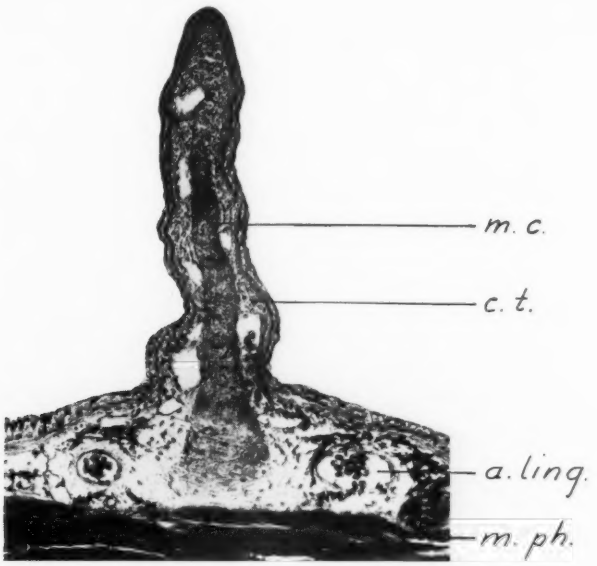

Fig. 16. Transversal section through the larval ventro-medial longitudinal bar. 140 ×.

musculus sublabialis (TRETJAKOFF 1929 a). On each side of the muco-cartilaginous bar, and on a level with its ventral surface, the two arteriae linguales (CORI 1905—06) run. This is seen in the photograph (fig. 16) showing a transversal section on a level with the caudal part of the musculus sublabialis. The other photographs illustrating the subsequent stages of development represent the same level.

The first visible signs of a beginning metamorphosis in the ventro-medial longitudinal bar do not concern the muco-cartilage but the surrounding connective tissue, (fig. 17), since, except for a thin collagenous layer nearest to the epithelium, the bundles of that connective tissue will gradually break down. The first trace of this process shows round the nuclei. Up to this moment the nuclei have been situated longitudinally in strong bundles of connective tissue and, for this reason, they have been difficult to discern. Now, they appear more distinctly in the preparations and, therefore, give an impression of having increased in number. The breaking-down of the fibrillar bundles continues and

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leaves eventually a tissue resembling an embryonic mesenchyma. This mesenchyma consists of intercellular substance, in which a three-dimensional network of plasma is embedded. The nuclei, which occur in a moderate number, are wrapped up in the fibres of this network.

The increase in number and the simultaneous enlargement of the blood vessels, which have taken place side by side with the above described process,

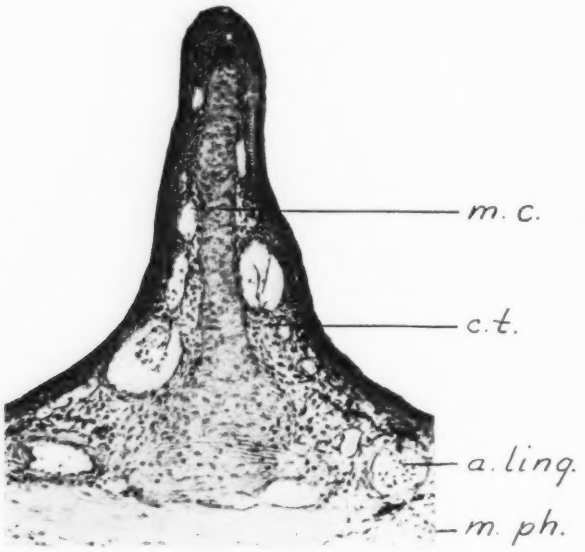

Fig. 17. Transversal section through the ventro-medial longitudinal bar. Early metamorphosis. 140 ×.

suggests a break-down under the possible influence of blood cells. However, isolated phagocytes have been observed only in the ventral parts, i.e. in the neighbourhood of the muscles in this area. Also the muscles have commenced to break down. DAMAS (1935) has stressed a fact that will be dealt with later, viz., that blood cells play an important part in the transformation of musculature. For these reasons, the bloodcells in the ventral region of the mesenchyma may, perhaps, take part exclusively in the last mentioned process. If so, the breaking-down of the collagenous bundles would be brought about exclusively by the tissue's own cells. There is, of course, a further possibility, viz., that both kinds of cells in this instance act more or less together in the ventral part, where they appear simultaneously. However this mesenchyma may be formed, its nuclei are considerably smaller and, on an average, more strongly stained than those of the cells of the muco-cartilage. Because of this, it is possible, during the remaining part of the process, to distinguish these two adjacent elements from one another.

While the process in question has begun in the parts adjoining to the muco-cartilage, the latter tissue has not visibly changed.

At a later stage, the process in the ventro-medial longitudinal bar has resulted in a considerable change in the shape, as will be seen from a comparison between figs. 17 and 18. The base has broadened, although the height remains practically unchanged. In the epithelium towards the cavity of the mouth

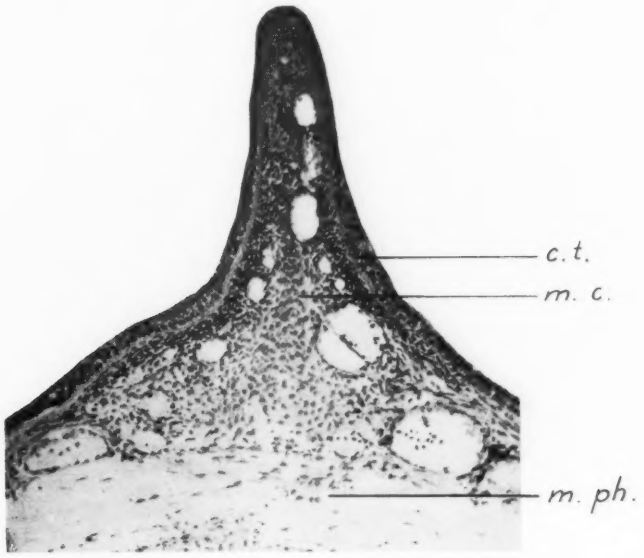

Fig. 18. Transversal section through the ventro-medial longitudinal bar. Metamorphic stage. 140 ×.

isolated mitoses are noticeable. The collagenous layer nearest underneath it seems unchanged. In the small-nucleated mesenchyma, immediately underneath this cell-layer, divisions are taking place. The extension of the mesenchyma has increased. This may naturally have contributed to the change in shape of the ventro-medial longitudinal structure.

But changes in the muco-cartilage itself have also contributed to this result. The muco-cartilage has broadened ventrally, while it appears to have almost the same extent dorsally. This change in the shape of the muco-cartilaginous complex has, however, been accompanied by a reduction in the stainability of the intercellular substance, especially in the ventral parts. Dorsally the structure of the muco-cartilage remains practically unchanged in this respect. The gradual participation of the cellular elements in this change can also be discerned. Dorsally the cell processes can still be distinguished. Ventrad their stainability diminishes, and, in the ventral parts, the processes have lost their

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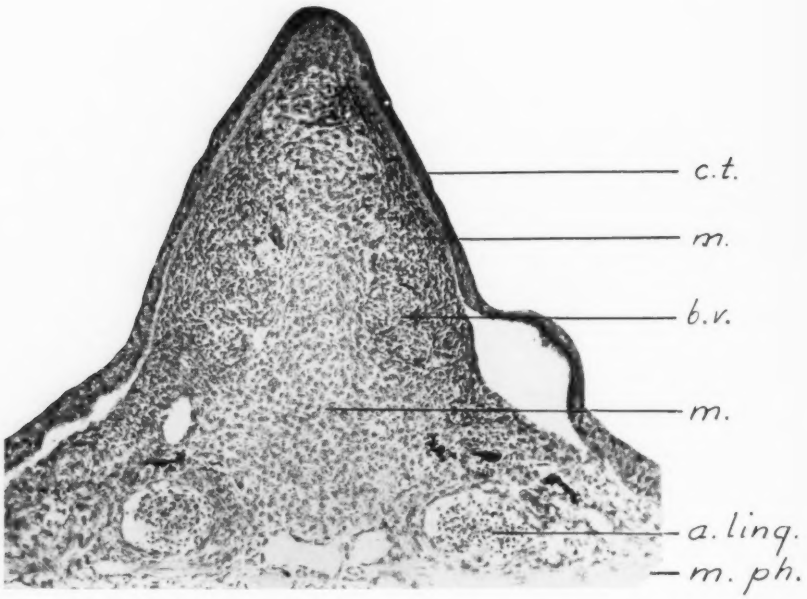

Fig. 19. Transversal section through the ventro-medial longitudinal bar. Metamorphic stage. 140 ×.

differentiation. There the tissue can almost be said to have assumed the character of a mesenchyma.

Ventrally the breaking-down of the musculature has continued. Among the muscular bundles, in which striated elements are still visible, free myocyte nuclei can be seen among the connective tissue cells. They can be distinguished from the others, at least at earlier stages, on account of their pronounced longitudinal shape. Also, they are larger than the average of the nuclei of the connective tissue cells.

At the next stage (fig. 19) the ventro-medial longitudinal bar is still broader ventrally, and the structure as a whole tends to sink into the considerably thickened body wall. In the center of the mesenchyma derived from muco-cartilage a first indication of a blastema can be discerned. Isolated cell-divisions have, probably, contributed to the formation of this blastema. However, the appearance of migrant cells within the muco-cartilage also seems to play a part in the formation of blastemas, as the nuclear divisions are considerably less frequent at these stages than later. The cells in the surrounding small-nucleated mesenchyma have also begun to divide to a certain extent. The development has at this point probably attained the state where DAMAS' description begins.

Dorsally and laterally, the mesenchyma with big nuclei is delimited from that with small nuclei, by an increasing number of blood vessels on the border surface between them. Possibly, the occurrence of blood vessels can have some rela-

tion to the reduction of the dorsal parts of the organ. This reduction appears also to be connected with its sinking-down into the floor of the mouth.

The nuclei in the large-nucleated mesenchyma have now attained a regular spherical or ovoid shape, while, originally, as stated above, they display a greater variety in outline. The "fibres conjonctives", mentioned above in a quotation from DAMAS, which, according to him, replace the elastic fibres during the transformation, are, indubitably, nothing but remaining dedifferentiated cellular processes. "Elles s'estompent de plus en plus jusqu'à devenir tout à fait invisibles."

Ventrally the destruction of the musculature proceeds. The small-nucleated mesenchyma, which in this place is, probably, derived also from the connective tissue that forms part of the musculature, is, in consequence, mixed with free myocytes. As stated above, the latter are, at least to begin with, distinguishable from other cells, on account of their markedly oblong nuclei. The two arteriae linguales, which in the larva are situated closely below the epithelium, are now separated from it, by a thick mesenchymal stratum, chiefly consisting of the forementioned small-nucleated cells mixed with phagocytes and free myocytes. The latter thus show a tendency towards wandering dorsad, laterally to the large-nucleated mesenchymatic area. They will probably later participate in the building up of different muscles in the rasping tongue. In the small-nucleated mesenchyma there will soon appear blastemas, for instance, of the sinew of the musculus cardio-apicalis that runs dorsally to the piston cartilage (TRETJAKOFF 1926 a), of the perimysia and of some ligaments connected with the final formation of the tongue roll.

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At a later stage the ventro-medial longitudinal bar has sunk still further into the ventral body wall (fig. 20). The arteriae linguales have deviated still more from the mucous membrane of the mouth cavity.

The blastema situated in the large-nucleated mesenchyma has become considerably more compact. Between the cells in the center are seen structures that are to be regarded as the first visible traces of the intercellular substance characteristic of cartilage. On the surface of the blastema the cells seem prolonged in a transversal section, parallel to the periphery of the blastema. They indicate the first stage in the development of a perichondrium. Cell divisions are common in all parts of the primordium. The blastema is entirely surrounded by a sparse mesenchyma in which blood vessels lie, at this stage not only dorsally but also ventrally to the blastema. The blood vessels dorsally situated which gradually fuse into larger lacunae will later form the blood sinus which dorsally and laterally surrounds the piston cartilage, and separates it from the dorsal part of the musculus mandibularis posterior and cardio-apicalis with its sinew (TRETJAKOFF 1926 a).

The difference described above between a central procartilage portion and a peripherally situated perichondrium has been further accentuated at a following

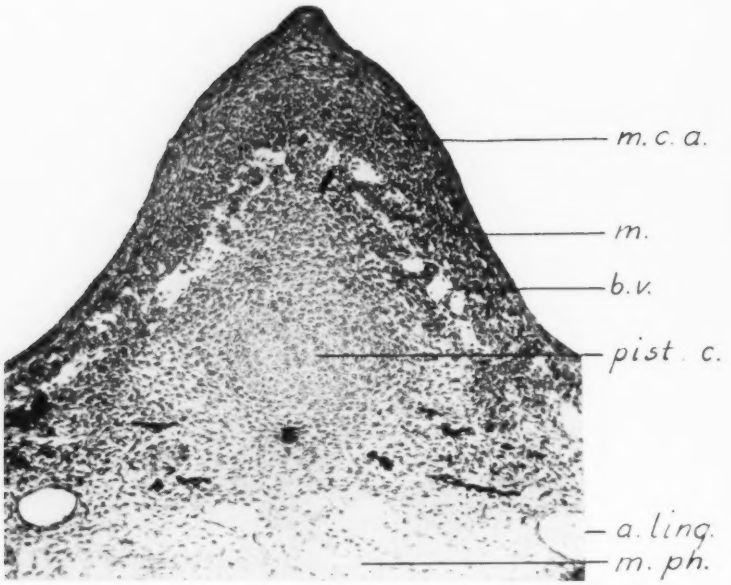

Fig. 20. Transversal section through the ventro-medial longitudinal bar. Metamorphic stage. 140 ×.

stage (fig. 21). The cell divisions are still frequent, though probably less in the center. Here, the tissue shows well developed cartilaginous capsules. In the periphery the cells lie less densely, and their processes are prolonged in a direction parallel with the periphery, being all the time easily observable.

The primordium of the piston cartilage thus formed lies buried in the thickened floor of the mouth cavity surrounded by various muscular blastemas. Dorsally the mesenchyma forms a blastema constituting the primordium of the dorsal part of the musculus mandibularis posterior (TRETJAKOFF 1926 a). Ventrally to this muscle, but dorsally to the piston cartilage, the primordium of the rostral sinew of the musculus cardio-apicalis is seen. The next photograph (fig. 22) shows the position at a subsequent stage. At this the blastema of the musculus mandibulariglossus (TRETJAKOFF 1926 a) and the ventral part of musculus mandibularis posterior are likewise to be seen.

The final formation of the piston cartilage is accomplished by a continuous formation of cartilage for yet a considerable period of time. Nothing new from a histological point of view is, however, to be seen.

In short, the process described above can be said to have taken place as follows: The intercellular substance of the muco-cartilage is transformed, while, simultaneously, the muco-cartilaginous fibres turn into undifferentiated protoplasmatic processes. Even before cellular divisions become noticeable to any noteworthy extent in the muco-cartilage, a concentration of cells takes

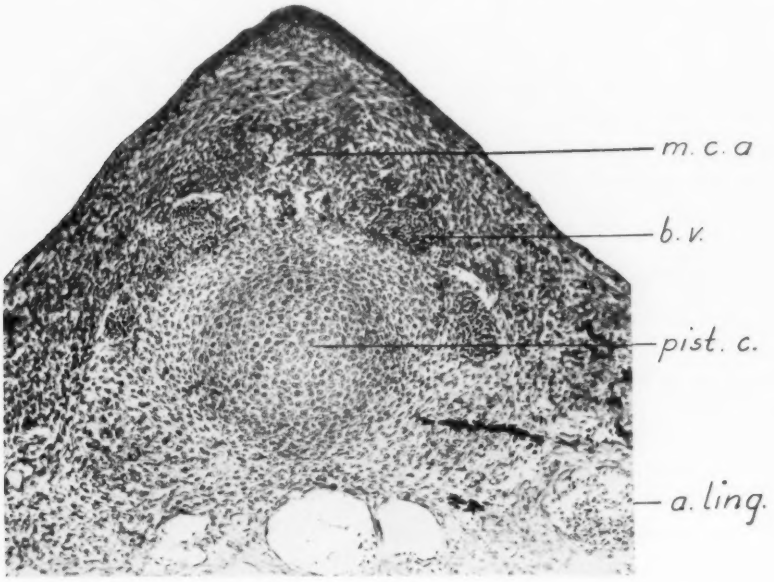

Fig. 21. Transversal section through the primordium of the piston cartilage. 140 ×.

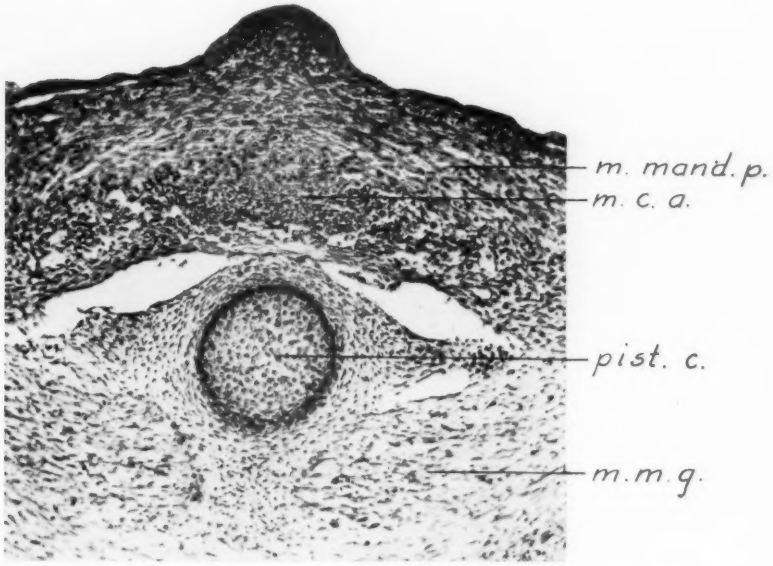

Fig. 22. Transversal section through the piston cartilage just formed. 140 ×.

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place in the center of the future cartilaginous structure. The blastema thus formed, therefore, appears to be, at least partly, the result of a cell migration. After that the blastema continues to grow by means of a lively process of cell divisions. On account of the gradually diminishing distance between the cells, the cellular processes by degrees diminish in length and, simultaneously, lose in stainability. Finally, the nuclei collect into a seemingly homogeneous mass in which the cartilaginous capsules afterwards develop. Attention is particularly drawn to the fact that phagocytes are not to be found in the cartilaginous blastema. This fact is worth noting as they regularly appear in such parts of muco-cartilage which do not change into cartilage and are later to disappear (see below). In addition, leucocytes are always seen in such blastemas which are going to develop into musculature.

b. *The breaking-down of muco-cartilage.*

When the piston cartilage is formed, as already described from a histological point of view, the main part of the muco-cartilage in the medio-ventral longitudinal bar is transformed into cartilage or perichondrium. Elsewhere, as a rule, only part of the muco-cartilage is used up, although the histological process itself always appears to be the same. As there is no trace whatever of this tissue in the full-grown animal, the question is what fate such parts will meet with as have not, in the course of metamorphosis, been transformed into cartilage. This problem was first observed by SCHAFFER (1896). However, he goes no further than to mention it. BUJOR (1890—92), on the other hand, writes as follows: "Après la destruction des parties déjà existantes chez l'Ammocoetes, l'espace rempli seulement de débris sans forme, est envahi par la lymphe et le sang."

DAMAS (1935, p. 195) has delivered a histological account of these processes. According to him it is evident that the disappearance of the muco-cartilage is the result of a process of complete annihilation. He writes: "La plus grande partie est enlevée, à la fin des transformations, par le creusement des sinus sanguins. Pour cela, les capillaires envahissent le tissu. Ils semblent dissoudre la substance fondamentale qui se désorganise à leur contact. Les vaisseaux deviennent de plus en plus vastes et nombreux. Ils confluent finalement, créant, par leur union, les sinus sanguins. Leur action histolytique doit être aidée par les leucocytes. En effet, on trouve dans le tissu conjonctif destiné à être enlevé et uniquement dans celui-ci, des nombreux globules blancs. Malheureusement, leur faible taille nous a empêche de faire à ce sujet des observations précises."

The present investigation has, however, afforded opportunities to collect some observations regarding the part played by leukocytes during this process. At early stages, when as yet no signs of any capillaries are to be seen in the muco-cartilage, isolated blood cells will, on the other hand, be found in the

tissue. They appear first in the surface areas of the muco-cartilage, gradually finding their way deeper into the tissue. As far as the ventro-lateral plate is concerned, the leukocytes in it appear to originate partly from the mesenchyma resulting from the demolition of the musculus pharyngeus, where leukocytes (see above) abound, partly from the subepithelial vascular plexus (HOLMGREN and STENSIÖ 1936) which is enlarged in the course of the metamorphosis. DAMAS' observation that leukocytes do not appear in such blastemas as later form cartilage should be particularly emphasized. Only after some time's activity by the leukocytes will an infiltration of blood vessels follow, the former process having, it would seem, paved the way for the latter one.

According to DAMAS, the matrix would be disorganized when getting into contact with the capillaries. Still, the stainability of the matrix will, as a rule, disappear even before any leukocytes have appeared in that particular tissue. Thus, the process is similar to the first phase of the transformation into cartilage. Occasionally, however, the basophilic property of the intercellular substance will remain in certain places, as, e.g., in the ventro-medial part of the ventro-lateral plate, notwithstanding the fact that a breaking-down of the muco-cartilage is to be found in its immediate vicinity. DAMAS' observations probably concern these comparatively late stages of the process.

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In connection with the forementioned process of disorganization, degenerating nuclei will appear in the muco-cartilage. Nucleolus and nuclear membrane will become indistinct and, finally, in the strongly diminished and irregularly shaped nucleus, defy all attempts at detailed observation. The nucleus is strongly stained. Soon the cellular processes lose their pronounced capacity of light refraction, while remaining relatively unchanged in extent. However, their surface grows more and more uneven and indistinct. Finally, the cell and cellular nucleus dissolve.

With certain exceptions, to be dealt with later, the nuclear frequency characteristic of the muco-cartilage will not change visibly during the different phases of the breaking-down process. In some rare instances, structures suggestive of mitoses have been noted, but the exact kind of cell that has been involved has eluded observation. At such early stages, viz., at the first appearance of blastemas, mitoses are exceedingly unusual. As previously discussed the blastemas will take form, at least partly, by means of cellular migration within the muco-cartilage. However, no reduction in the nuclear frequency of the tissue surrounding the blastemas has been observed. The extent of this possible migration of cells for that reason remains obscure.

Within certain restricted parts of the muco-cartilage, its disappearance is connected with a more complicated process than that described above. The intercellular substance will first vanish, in the manner previously described. However, this process will be accompanied by a conspicuous increase in nuclear frequency, as happens in the parts that turn into such blastemas as form into

cartilage. Cellular divisions occur regularly, though possibly less often than in the cartilaginous blastemas. A great many of the nuclei become intensely stained and display a regular, oval outline. As no symptoms of nuclear degeneration will appear until very late, these nuclei may have reached a phase corresponding to the transitional stage in the formation of cartilage, when the affinity to nuclear colours is markedly accentuated, as first observed by SCHAFFER (1896).

These blastema-like structures are always united with real blastematic primordia forming cartilaginous elements which they connect or are processes from. In the present investigation no histological differences between these structures and real blastemas have been distinguishable at earlier stages. However, they do not give rise to cartilage but disappear later, leaving no trace.

While the cells in real blastemas continue to develop, these blastema-like structures remain at the same stage of development for a considerable space of time (cf. the descriptions of stages). Gradually, however, real signs of degeneration appear. The nucleus looks indistinct. Nucleus membrane and nucleolus vanish. Finally, the entire nucleus is intensely stained, without any differentiation. The structures now decline in extent. At late stages the tissue will sometimes become disorganized through the appearance in it of blood cells. It may, however, be noted that a large part of the metamorphosis has passed before the breaking-down process commences.

c. *The formation of cartilage in fibrous connective tissue and growth of cartilage.*

In the course of metamorphosis cartilage will form also in places where no muco-cartilage can be supposed to constitute the original material (cf. p. 239). This happens, e.g., in certain parts of the connective tissue capsule that envelops the central nervous system. In addition, certain cartilaginous elements, as, for instance, the annular cartilage and the anterior cartilage, are established in areas which, in the larval stage, are rich in musculture.

As stated—as early as by SCHNEIDER (1879)—the musculature is, in the latter case, broken down, the process in this instance being analogous to that dealt with, in passing, in Chapter IV, 1. This process has been described from a histological point of view by DAMAS (1935). The breaking-down will result in an embryonic "tissue conjonctif" in which the new muscles will develop as "néoformations". A similar, though not very detailed account, is delivered by KAENSCHE (1890), while SCHNEIDER (1879) and BUJOR (1890—92) adopt the view that the dissolved musculature is replaced by tissue elements from the muco-cartilage which, in their turn, give rise to cartilage as well as to musculature.

It may be accepted as certain that muco-cartilage does not play any part in the formation of the new tissues in these areas. If it did, comprehensive transports of material would be necessary. However, no trace of such processes has been observed. In accordance with DAMAS' (1935) thesis, mesenchyma, arisen through a dedifferentiation of musculature, would rather be the source of both cartilage and musculature.

The first symptom of a disorganization of the musculature manifests itself in a transformation of the connective tissue cells in the perimysia into mesenchyma of an embryonic type. No doubt, the following breaking-down of the muscular bundles is effectuated by means of blood cells, as suggested by BUJOR (1890—92), among others. However, only the striated fibres themselves are destroyed. In the present investigation nothing has been observed that proves the nuclei of the muscular cells to be affected. As mentioned earlier these nuclei are, to begin with, easily distinguished from connective tissue nuclei, being larger and of a considerable length. The nuclei of the connective tissue are, on the other hand, spherical or faintly ovoid. Further, no dissolving of connective tissue nuclei has been observed by the present author. Thus both kinds of cells seem to exist together in the mesenchyma. Later, cartilage and connective tissue are, as indicated by DAMAS (1935, 1944), probably derived from the connective tissue cells, while the myocytes form the muscular fibres.

Differentiated connective tissue cells change into cells of an embryonic type also when cartilage is formed in fibrous connective tissue. The often powerful bundles of fibres dissolve and certain cells soon assume an embryonic character. They may afterwards be transformed into procartilage even before all the fibrous elements in the vicinity have dissolved completely. This kind of cartilage formation has been described in detail by SCHAFFER (1896, 1897, 1901, etc.) and STUDNIČKA (1897, 1898 a, b, etc.) but also by KAENSCHE (1890), BUJOR (18890—92), DAMAS (1935) and HOLMGREN and STENSIÖ (1936).

The cartilage so formed will in certain places give rise to new elements, in others, it causes an appositional growth of the larval cranium. LANGERHANS (1873), and others, have pointed out that the larval and the later skeletal elements remain discernible in the full-grown Petromyzon.

The outlines of the larval portions in the nasal capsule indicate, as is seen from the reconstructions (figs. 26, 45), a gradual increase in size. This is due to an interstitial growth which occurs simultaneously with the appositional growth. As far as can be seen, a special type of interstitial growth, easily observed histologically, has been left unnoticed by earlier investigators.

This histological process begins with the dissolving of the intercellular substance in the cartilage during which the tissue is transformed into mesenchyma of embryonic type. In mesenchyma thus formed cartilage develops which causes an increase in volume of the tissue. However, it hardly seems possible to attribute the entire interstitial growth of the nasal capsule ex-

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clusively to this process, since it takes place only at certain comparatively early stages of metamorphosis. This unusual form of growth of cartilage has been noticed both in the nasal capsule (fig. 23) and in the pedicle.

Also the normal type of interstitial growth of cartilage is observed in the cartilaginous cranium (SCHAFFER 1896, 1901) and will, inter alia, account for part of the increase in volume found in the nasal capsule. The less thorough changes of trabecles and auditory capsules are caused by this normal type of

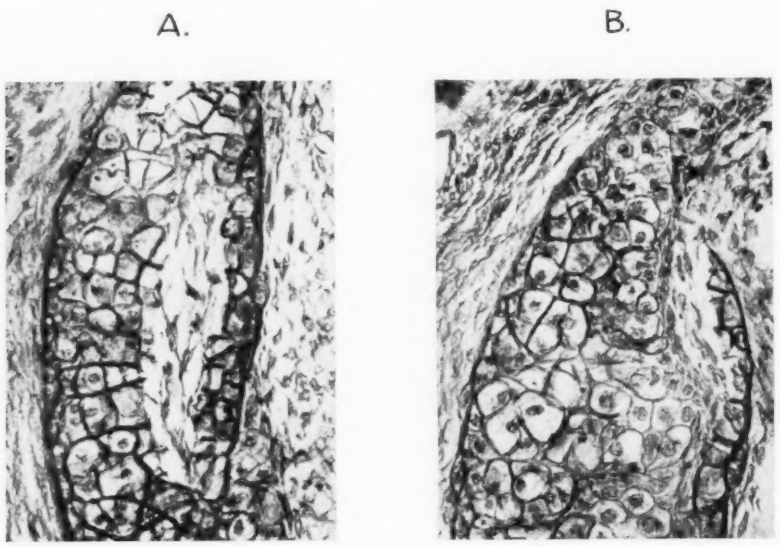

Fig. 23. Metamorphic stage. Transversal section through the left part of the olfactory capsule. A. Dissolving intercellular substance in cartilage. The free cells form mesenchyma. B. Forming of cartilage in mesenchyma between remaining parts of larval cartilage. 350 ×.

growth. As previously stated, the growth within the various cartilaginous elements formed in the course of metamorphosis manifests itself through lively cell divisions both centrally, within cartilage and procartilage, and in the peripheral, less differentiated, parts.

2. DESCRIPTION OF STAGES.

a. *Stage 1.* (Diameter of the eye 1120 μ.)

At this stage only slight metamorphic changes have taken place.

The stainability of the matrix in certain places of the muco-cartilage has diminished or disappeared. This applies to the free edge of the ventro-lateral plate, partly immediately rostrally, partly slightly medio-caudally to the ventral

longitudinal bar of the branchial basket. Otherwise the muco-cartilage in the ventro-lateral plate remains unchanged. From the point of attachment of the ventro-lateral plate and caudad, the stainability of the matrix of the subotical muco-cartilage mass gradually decreases. In the caudal portion, directly adjoining to the first branchial arch, the stainability has entirely vanished. The same changes take place in the muco-cartilage around the trabecular commissure and the adjoining caudal part of the rostro-dorsal plate, as well as in the rostral part of the subocular muco-cartilage portions. The change is most pronounced in the vicinity of the trabecular commissure.

The muscle complex that separates the muco-cartilage in the caudal part of the rostro-dorsal plate from the laterally situated rostral part of the subocular muco-cartilage portion (musculus depressor labii superioris, acc. TRETJAKOFF 1929 a, "releveur de la lèvre postérieur", acc. DAMAS 1935) shows the first signs of an incipient break-down. Around the muscular bundles, which are apparently still intact, nuclei accumulate. This accumulation is probably caused by the begun dissolution of the connective tissue that surrounds the musculature. Similar processes have, likewise, commenced in the musculature directly adjoining to the caudo-ventral parts of the rostro-dorsal plate (musculus buccalis, TRETJAKOFF 1929 a, DAMAS 1935).

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b. *Stage 2.* (Diameter of the eye 1350 μ.)

The breaking-down of the intercellular substance of the muco-cartilage and the dedifferentiation of connective tissue have continued in the places mentioned above.

The caudal portion of the buccal musculature and the part of the musculus depressor labii superioris situated between the caudal part of the rostro-dorsal plate and the subocular muco-cartilage portion show more marked signs of dissolution (fig. 24), since, now, also the muscular fibres themselves have been attacked. The muco-cartilage close to this musculature has turned into mesenchyma, where the frequency of cells exceeds that of the muco-cartilage. Considering that at this stage no cell divisions take place in the muco-cartilage, the accumulating cells probably originate from the connective tissue round the muscle fibres. In this tissue, cell divisions are common. In the muco-cartilage in the medio-velar skeleton, the cells concentrate towards the centre. Contrary to the normal process this does not seem to be preceded by any disorganization of the matrix of the tissue.

At this stage, the subepithelial connective tissue round the muco-cartilage in the ventro-medial longitudinal bar is seen to be in an early state of dissolution (cf. p. 178).

An incipient break-down is also visible in the connective tissue band which,

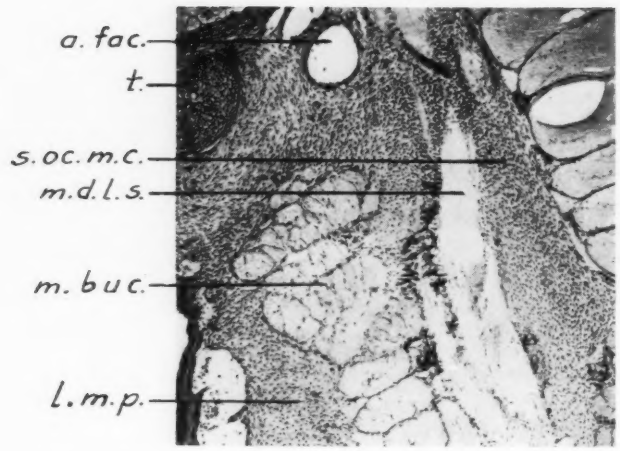

Fig. 24. Metamorphic stage 2. Transversal section through a part of the right body wall, immediately caudally to the trabecular commissure. 70 ×.

ventrally to the eye, connects the subocular muco-cartilage portion with the muco-cartilage round the pedicle process (fig. 25. "Thickened bar of the orbital capsule", HOLMGREN 1943 a).

c. *Stage 3.* (Diameter of the eye 1230 μ.)

In the dorso-caudal edge of the ventro-lateral plate the changes of muco-cartilage have proceeded so far dorsad as to bring the mesenchyma, originating from it, into contact with the mesenchyma that has, simultaneously, arisen from the subotical portion of muco-cartilage. Rostrally, the latter portion of mesenchyma surrounds the pedicle and joins the caudal part of the mesenchyma formed from the connective tissue band situated ventrally to the eye. The dorsal part of the lateral velar skeleton, which fuses with the muco-cartilage portion that unites the ventro-lateral plate and the subotical muco-cartilage portion, has changed in the same way. The number of nuclei in the subotical mesenchymatic mass and in the ventral parts of the lateral mouth plates has increased.

Otherwise, this stage does not in any noteworhthy degree differ from the conditions previously described.

The above-described processes prepare, through a disorganisation of larval tissues, the subsequent development of the primordia which arise during the metamorphosis. In certain instances mesenchymatic areas have formed, the derivation of which can only be determined by a study of earlier stages. In some cases, though, remaining fragments of larval tissues may provide sufficient information in this respect. Once the transformation has proceeded as far as to the formation of mesenchyma, there is no possibility to distinguish histologically what has previously been a muco-cartilage from mesenchyma that

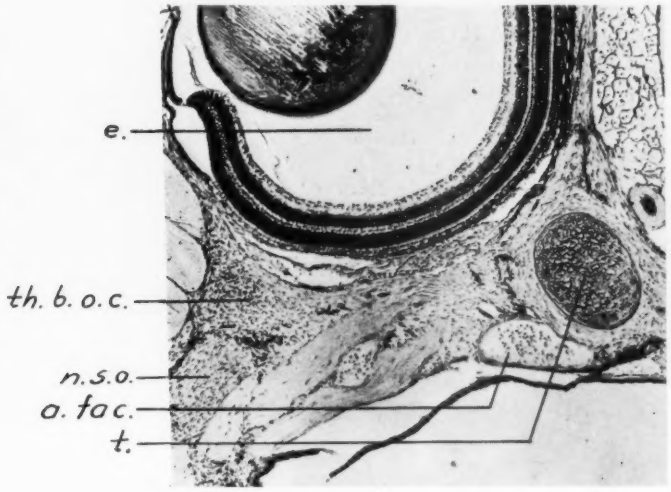

Fig. 25. Metamorphic stage 2. Transversal section through the region ventrally to the left eye. 70 ×.

develops from connective tissue. Isolated myocytes can, as previously mentioned, be distinguished from the connective tissue cells. The myocytes probably constitute the foundation of the muscle blastemas and migrate to places where the blastemas are being formed. However, these migrations do not seem to be of any considerable extent, since the definite muscles are, for the most part, developed where larval musculature has previously been found (cf. DAMAS 1935).

d. *Stage 4.* (Diameter of the eye 1390 μ, cf. reconstruction fig. 26.)

Caudally, the muco-cartilage between the ventral longitudinal bars in the branchial basket has changed into mesenchyma. Also in the rostro-lateral parts of the ventro-lateral plate, the process of dissolution has become accentuated. In the medial portion, however, the matrix remains unchanged. Ventro-laterally, on each side of the median line, primordia of parietal musculature (musculus subocularis, TRETJAKOFF 1926 a) grow rostrad. Muco-cartilage in contact with these primordia dissolves (cf. DAMAS 1935, p. 202 ff.).

While in the rostral parts of the rostro-dorsal plate the muco-cartilage is unchanged, the mesenchyma in the caudal parts has expanded further, in comparison with the preceding stages, coming into contact with the mesenchymatic lateral mouth plates. There, the matrix has lost its stainability, as well as in the medial and lateral velar skeleton, the ventro-medial longitudinal bar and the muco-cartilage in the branchial basket.

In addition to the musculature mentioned earlier, also that situated ventrally

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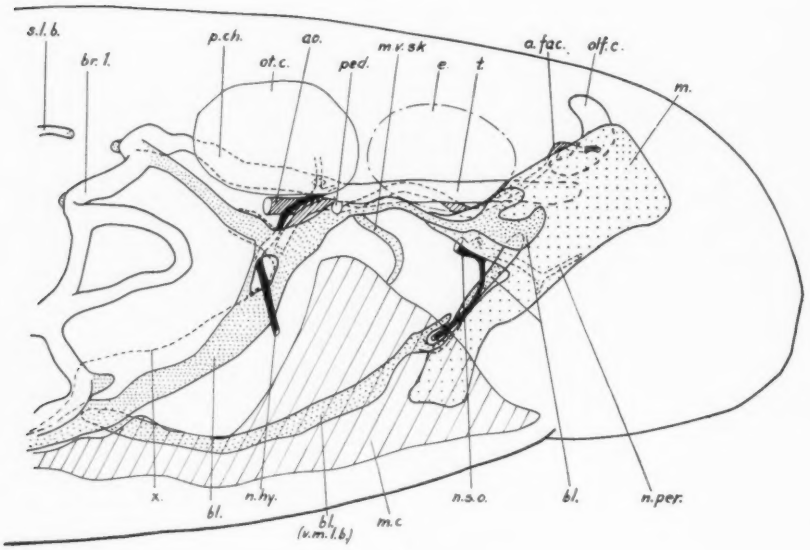
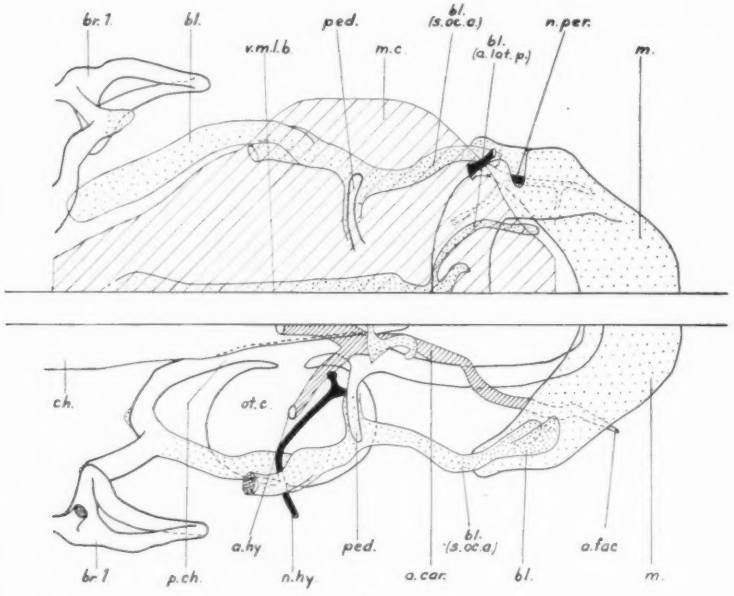


A.



B.

Fig. 26. Metamorphic stage 4. Reconstruction of skull. A. Lateral view, B. Ventral view. Above ventral parts, below dorsal parts of the skull.—Densely dotted area indicates blastema. Sparsely dotted area indicates mesenchyma. Sparsely striped area indicates unchanged muco-cartilage. Blood vessels are densely striped and nerves are black. Contours of cartilage elements are shown by continuous lines. 15 ×.

to the eye (musculus buccalis posterior superficialis, TRETJAKOFF 1929 a, DAMAS 1935) has begun to dissolve (fig. 27). In connection with this process, the scattered nerve fibres in the last-mentioned musculature begin to collect into a nerve (nervus basilaris, TRETJAKOFF 1927 a), a process that continues slowly for a considerable time, simultaneously with the dissolution of the muscular bundles. In the rostral buccal musculature (musculus buccalis anterior,

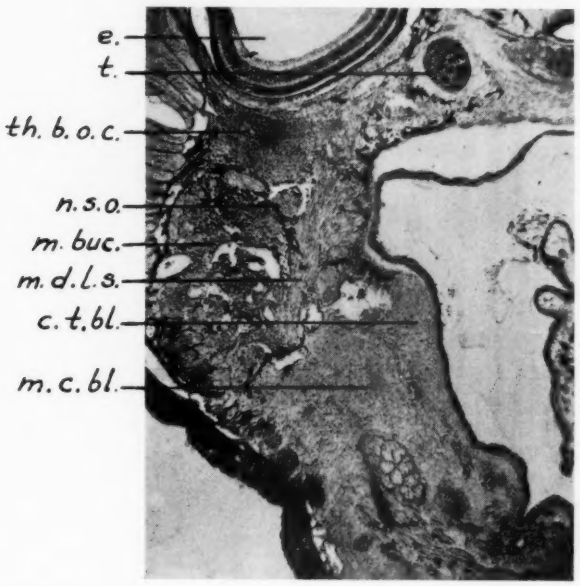


Fig. 27. Metamorphic stage 4. Transversal section through the left body wall, on a level with the point of fusion between the lateral mouth plate and the ventro-lateral plate. 35 ×.

TRETJAKOFF 1929 a) the disorganization has extended rostrad, concentrating to the region of the nervus apicalis (TRETJAKOFF 1927 a) and dorsally to it. Immediately rostrally to the thyroid gland, the caudal part of the pharyngeal musculature (musculus constrictor prebranchialis, TRETJAKOFF 1929 a, musculus constrictor pharyngei, DAMAS 1935) forms a particularly pronounced accumulation of muscular bundles. A tendency to disorganization can be discerned in this place.

In three places in the larva the muco-cartilage is separated from the mucous membrane in the cavity of the mouth by well developed connective tissue. This is the case medially to the lateral mouth plates (fig. 27), medially to the thickened edge of the ventro-lateral plate, and dorsally and laterally to the ventro-medial longitudinal bar. A considerable part of the connective tissue in these places has changed into polynuclear mesenchyma with but a thin stratum of collagenous connective tissue remaining immediately below the epithelium.

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At this stage cell concentrations have taken place in certain of the previously mentioned mesenchymatic areas. For the greater part, these structures constitute the first primordia of the organs of the full-grown animal. It is impossible to determine the exact limits of such blastemas owing to their diffuse character. Naturally, the histological features peculiar to a specialized tissue are lacking in the early stages. In the reconstructions presented in this chapter the approximate extent of these blastemas is indicated.

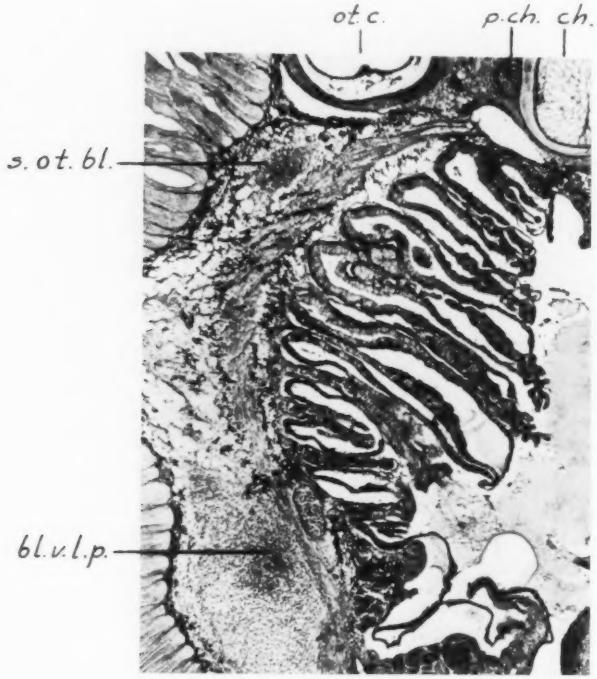

Fig. 28. Metamorphic stage 4. Transversal section through the left body wall, on a level with the rostral part of the auditory capsule. 35 ×.

Ventrally to the auditory capsules, a blastema forming in the subotical portion of muco-cartilage extends from the dorsal part of the first branchial arch to the pedicle process (fig. 28). Medially to this, the nervus glossopharyngeus and nervus hyoideus (TRETJAKOFF 1927 a) run ventrad. In the caudal parts the earlier outline of the muco-cartilage can no longer be distinguished, since the surface tissue has changed into mesenchyma. Nothing but a dense blastema remains of the relatively voluminous muco-cartilage mass. Ventrally to the auditory capsule, another blastematic bar proceeds in a curve from this blastema, being directed towards the ventral part of the first branchial arch (fig. 28). In the vicinity of this arch the blastema becomes diffuse and

changes gradually into the mesenchyma developed between the ventral longitudinal bars.

The ventral blastema is split into two parts in the neighbourhood of its point of juncture with the subotical blastematic portion. Between these parts the nervus hyoideus runs (TRETJAKOFF 1927 a, N. hyomandibularis, JOHNSTON 1905) from the medial side laterad to the blastema. In the larva this nerve runs immediately caudally to the ventro-lateral plate. Thus the part of the blastema situated caudally to the nerve must have been formed outside the muco-cartilage (fig. 29). Round this part of the blastema the transitional tissue, previously described in Chapter III, has turned into mesenchyma and, in consequence, the former border-line between the muco-cartilage and the forementioned tissue has been blotted out.

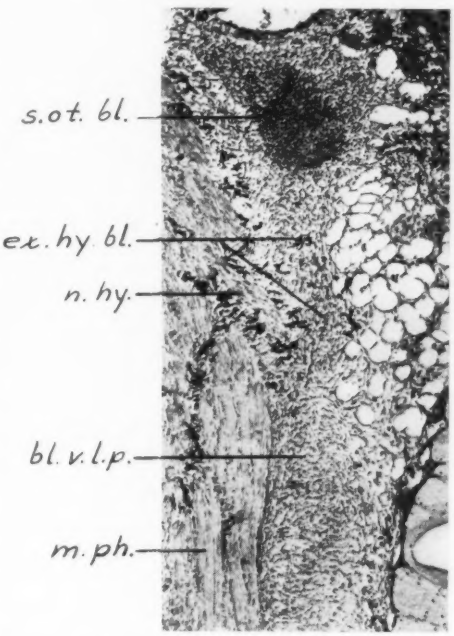

Fig. 29. Metamorphic stage 4. Transversal section through the right body wall showing the blastema caudally to the nervus hyoideus. 70 ×.

On the other hand, the part of the blastema that is situated rostrally and ventrally to the nervus hyoideus lies entirely within the limits of the earlier existing muco-cartilage. The mesenchyma formed by the connective tissue which, in the larva, lies medially to the muco-cartilage, reveals a tendency to fuse with the mesenchyma formed by the muco-cartilage (fig. 30). In addition, the mesenchyma is denser in its medial side than elsewhere. These processes are most advanced in the parts closest to the pedicle. They also extend to the rostral part of the subotic blastema portion. The part of the blastema situated caudally to the nervous hyoideus seems to have been formed there by connective tissue cells, as no migration of cells from the muco-cartilage has been observed.

From the pedicle the blastema continues rostrad, ventrally to the eye (fig. 27). It has its origin in the mesenchyma formed from the breaking-down of the connective tissue bar in this place. Ventrally to the middle part of the eye the blastema runs into a mass of mesenchyma in which it can be distinguished rostrad as a dense accumulation of cells. Rostrally and ventrally, the surrounding mesenchymatic area has an extensive range, a matter to be dealt with later.

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Fig. 30. Metamorphic stage 4. Transversal section through the left body wall showing the blastema caudally to the pedicle. 70 ×.

The rostral part of this subocular portion of blastema is divided into two branches, one dorsal, the other ventral. The dorsal one is directed towards the trabecular commissure which, however, it does not reach. Here the blastema passes through the dorsal parts of a dissolved muscle ("releveur de la lèvre posterieur", DAMAS 1935), and, in spite of the fact that the blastema is otherwise apparently homogenous, some fragments of as yet not dissolved muscular fibres are contained in it. Medially to the muscle the blastema fades away into the mesenchyma which has been formed from the caudal parts of the rostro-dorsal plate in the region of the trabecular commissure.

The ventral branch of the subocular blastema is, rostrally, bent dorso-rostrad. This branch, as well as that part of the dorsal one that lies laterally to the musculature ("releveur" etc.) probably is formed by the subocular muco-cartilage portion. The ventral and rostral portions of the blastema are in contact with mesenchyma from musculature in a state of dissolving.

The rostral mesenchymatic area into which the rostral parts of the subocular portion of blastema project is connected with the corresponding ventral part under the mouth. This ventral part is formed by the ventral portions of the lateral mouth plates and by the commissure which unites the mouth plates ventrally to the median tentacle. Dorsally the rostral mesenchymatic area comprises also parts formed by muco-cartilage connecting the lateral mouth plates

and the edge of the ventro-lateral plate (fig. 27). The musculature in this region (the rostral part of the musculus sublabialis. TRETJAKOFF 1929 a, and the ventral part of "releveur" etc., DAMAS 1935) is also partly dissolved.

While the mesenchyma at the place where the lateral mouth plate and the edge of the ventro-lateral plate meet has come close to the surface of the body, its dorsal and rostral parts lie deeper. Broadly speaking, the ventro-rostral boundary of the mesenchymatic area coincides with the line that is formed by the bases of the lateral tentacles where they join the ventral side of the upper lip. In that part of mesenchyma the nervus apicalis branches. Dorsad the mesenchyma extends through the dissolved buccal musculature. The dorsal portions of the mesenchymatic area develop from the caudal parts of the rostro-dorsal plate and the subocular muco-cartilage portion. Thus, the mesenchyma is connected with the trabecular commissure, as well as with the ventral and ventro-lateral sides of the nasal capsule.

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Like the buccal musculature between the tentacular bases and the dorsal parts of the mesenchymatic area, the musculature dorsally to the medial branch of ramus maxillaris trigemini (JOHNSTON 1905) is rapidly dissolving. Of this musculature (musculus buccalis superficialis, TRETJAKOFF 1929 a) only slight fragments remain.

The here described mesenchymatic area is formed from cells originally liberated from muco-cartilage, from musculature and from collagenous connective tissue. In places, where muscles will later develop, also blood cells will aggregate (cf. later descriptions of stages). Laterally and rostrally to the mesenchymatic area, larval musculature remains, and, rostrally to it, also muco-cartilage.

In its dorsal part the mesenchymatic area is in close contact with the arteria facialis (HATTA 1922—23, "Carotis facialis", CORI 1905—06). This artery runs from the medial side of the trabecle, ventrally to it, and then turns chiefly rostrad. In so doing it takes a course medially to the lateral part of the mesenchymatic area, as well as to the rostral part of the subocular blastematic portion situated in this area. When the mesenchyma in the region of the trabecular commissure has fused with the cartilage, the arteria facialis continues dorsally to this part of the mesenchyma, medially to its dorso-lateral edge. On a level with the nasal capsule the artery turns rostro-laterad, passes through the mesenchymatic area, and continues rostrad in the remaining muco-cartilage.

The ramus maxillaris of the nervus trigeminus (JOHNSTON 1905), which runs rostrad ventrally to the subocular blastematic portion, also gets into contact with the rostral mesenchyma. On a level with the place where the subocular blastematic portion forms two branches, the nervus maxillaris is divided in a lateral and a medial branch. Somewhat rostrally also a ventral branch is formed. It runs towards the base of the medial tentacle. The medial branch

passes rostrad within the mesenchymatic area and forms, as previously stated, smaller branches, on a level with the ventro-rostral boundary of the mesenchymatic area. Along its entire length this nerve (nervus apicalis, TRETJAKOFF 1929 a) is enveloped in mesenchyma, derived from adjacent, dissolved musculature and connective tissue. The ventral branch runs medially to the mesenchyma in the lateral mouth plate (see below).

In the medial velar skeleton the intercellular substance has disappeared, the tissue having assumed a mesenchymatic appearance. The concentration of nuclei towards the centre of the muco-cartilage, noticed at earlier stages, forms a blastema in the centre of the mesenchyma (fig. 31). Dorsally, the mesenchyma fuses with the cartilage in the trabecles, on a level with the pedicle process, and laterally to the arteria carotis (HATTA 1922—23). Ventrally to the two carotids and to the tip of the notochord, the medial commissure has changed into mesenchyma.

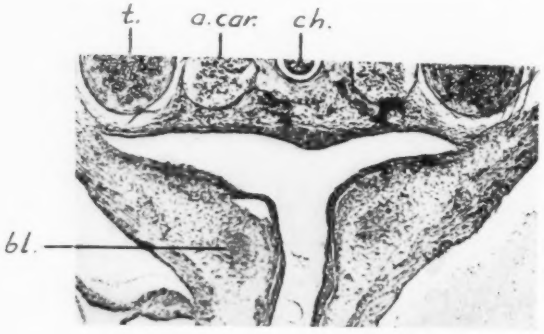

Fig. 31. Metamorphic stage 4. Transversal section through the dorsal part of the medial velar skeleton. 70 ×.

In the dorsal and lateral parts of the lateral velar skeleton blastemas have developed. The blastemas are separated from one another through parts where the cells are fairly sparse. In the medial parts the matrix is unchanged.

In the ventro-medial longitudinal bar the metamorphic processes have produced a condition corresponding to the stage described on p. 180. The blastema in the centre of the muco-cartilage portion previously situated here has assumed the shape of a longitudinal bar with an almost circular transverse section. Rostrad, the blastema continues into the base of the medial tentacle where it terminates in two short processes, one on each side. At the tentacle base two additional lateral processes proceed into the body wall, then continuing dorso-rostrad. This blastema is comparatively extensive. It derives from cells from the thick connective tissue (fig. 27) that cover the medial side of the lateral mouth plates. The mesenchyma in the lateral mouth plates remains distinctly separate from it. The nerve branch, previously referred to, that runs to the base of the medial tentacle, passes between the forementioned lateral processes and the mesenchyma in the lateral mouth plate.

The fibrous connective tissue which, together with the cartilage, surrounds the nasal sac has, close to the edges of the cartilaginous capsule, changed into blastema.

The muco-cartilage in the branchial region is absorbed by the more or less diffuse mesenchyma which fills up the space between the cartilaginous bars. These changes will be dealt with in the description of later stages.

c. *Stage 5.* (Diameter of the eye 1440 μ, cf. reconstruction fig. 32.)

This stage differs comparatively little from the preceding one. However, certain extensions of the blastematic portions and changes in their positions are noticed.

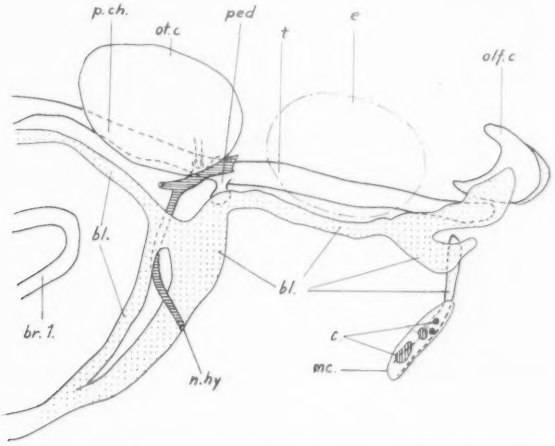

Fig. 32. Metamorphic stage 5. Reconstruction of parts of the skull. Lateral view. Dotted area indicates blastema. Cartilage nodules (*c.*) and the area of peculiarly developed muco-cartilage (*mc.*) are shown. Nervus hyoideus densely striped. 15 ×.

The blastematic complex round the nervus hyoideus has moved somewhat rostrad. Further, the split in the blastema round the nerve, which at the preceding stage was indistinct, has become more conspicuous. Ventro-caudad this division of the blastema remains even now diffuse. The blastema has extended caudad. Laterally to the thyroid gland, it is in contact with the medial side of the ventral longitudinal bar. The caudal part of the musculus velo-thyroideus (TRETJAKOFF 1929 a) extends between the connective tissue capsule of the thyroid gland and this blastema. This muscle forms a break in the continuity of the pharyngeal musculature which, otherwise, constitutes a coherent muscular stratum, running from one side to the other, dorsally to the muco-cartilage of the ventro-lateral plate. There are no muscles ventrally to the thyroid gland. Here the mesenchyma, developed from the muco-cartilage between the ventral longitudinal bars, now spreads.

Rostrally, the subocular blastematic portion has enlarged, particularly the dorsal branch. This branch has now expanded medio-rostrally and fuses with the trabecular commissure. It also reaches contact with a new-formed blastema

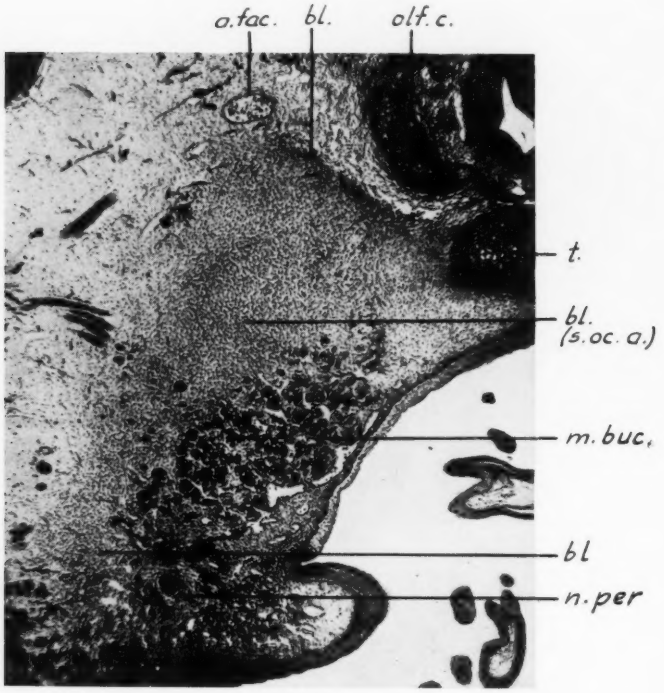

Fig. 33. Metamorphic stage 5. Transversal section of the left part of the head on a level with the trabecular commissure. 60 ×.

which stretches latero-dorsad from the trabecular commissure. This blastema is a wing-shaped structure (fig. 33) which has developed in the dorsal part of the rostral mesenchymatic area which, in its turn, as stated in Stage 4, has formed in the muco-cartilage in the caudal part of the rostro-dorsal plate. The arteria facialis runs caudally and dorsally to these blastemas. Thus, the relations are the same as those of the mesenchymatic portion at the preceding stage. Also the ventral one of the two branches of the subocular blastema has grown, as is obvious from the fact that it has deviated rostrad, thus getting closer to the region of the trabecular commissure.

Apart from an enlargement of the blastematic part of the connective tissue of the nasal capsule, there are otherwise no essential changes to be noted.

The cartilage of the nasal capsule, in which an interstitial growth (p. 187) takes place, is extraordinarily extensive. Also in another respect the specimen examined displays an abnormal development of cartilage. As briefly stated before (cf. Chapter III), cartilage has been observed in two specimens in the ventral parts of the lateral mouth plates. In one case there was only a small cartilaginous ball on one side. In the now described specimen a series of such

balls were found on both sides. While the first-mentioned specimen still displays larval conditions, this one shows signs of metamorphosis. Still, this fact, undoubtedly, lacks significance with regard to these aberrations in the muco-cartilage. While the metamorphic changes had only resulted in the formation of undifferentiated blastematic primordia, the balls consisted of well developed cartilage.

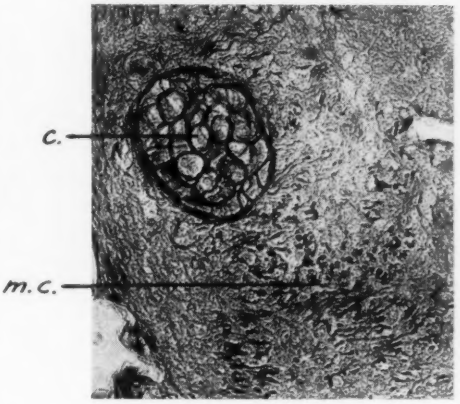

Fig. 34. Metamorphic stage 5. Section through cartilage nodule and peculiarly developed muco-cartilage in the lateral mouth plate. 240 ×.

The muco-cartilage in the region of those cartilaginous elements (4 on one side and 3 on the other) has a specific character (fig. 34). The cell processes are unusually well developed, hereby distinguishing this kind of muco-cartilage from the normal. In this specimen muco-cartilage of the same type will be found in the neighbourhood of the blastema ventrally to the pedicle and rostrally to the nervus hyoideus. Also in a few other specimens a similar formation has been noticed in the same places in the muco-cartilage.

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f. *Stage 6.* (Diameter of the eye 1620 μ, cf. reconstruction fig. 35.)

At this stage the first more general signs of destruction of muco-cartilage not engaged in forming blastema will appear. Accumulations of blood cells, often situated in small vessels or sinusoid blood lacunae, will be noticed in the rostral and ventro-medial regions of the ventro-lateral plate, i.e. the particular area which, in Stage 4, comprised unchanged muco-cartilage. This is the case also in the rostral parts of the rostro-dorsal plate. This infiltration is especially pronounced in the vicinity of dissolving muscles. Practically all visceral musculature in the rostral parts of the head has reached this stage. However, as could be seen from the description of Stage 4, the breaking-down process is not synchronous. It is not simultaneous even in one and the same muscle. Thus, large parts of the buccal muscles remain, for instance, rostrally and laterally in the upper lip. Only in the neighbourhood of the subocular blastema and the rostral mesenchymatic area, homogeneous mesenchyma (fig. 36) is the result of the dissolving process. In the pharyngeal musculature the breaking-down almost exclusively sets in from the surface adjoining to the muco-cartilage. In the course of this process, both these tissues are being infiltrated by blood vessels. This concerns especially the musculature ventrally to the ventro-medial longitudinal bar and the muscle bundles rostrally to the thyroid

gland. Rostrally, also the musculus sublabialis (TRETJAKOFF 1929 a, "rétracteur des papilles", DAMAS 1935) is partly demolished.

In the rostral mesenchymatic area blastemas have developed in certain places. The mesenchymatic area itself has grown in extent.

The division between the two blastemas, situated anteriorly and posteriorly to the nervus hyoideus, ventrally to the auditory capsule, is now more marked. Procartilage has developed in the subotical blastematic portion dorsally to the

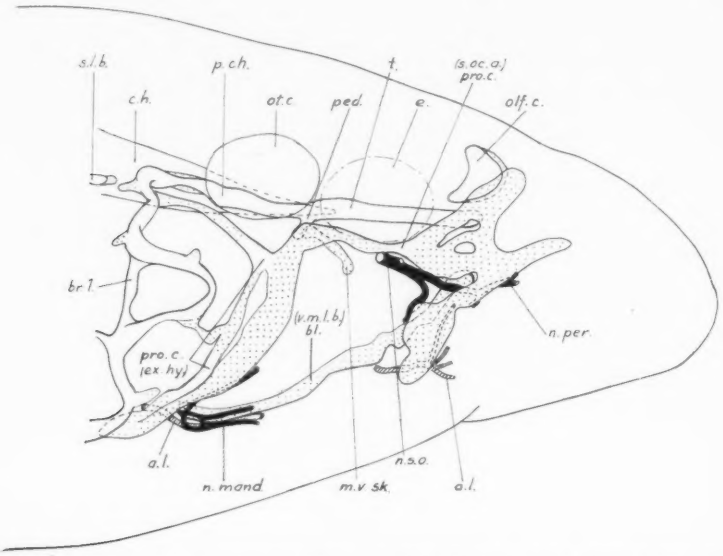

Fig. 35. Metamorphic stage 6. Reconstruction of skull. Lateral view. Dotted area indicates blastema. Contours of cartilage elements indicated by continuous lines. Nerves and vessels as in fig. 26. 10 ×.

nerve. That is the case also in the ventral part of the blastematic portion situated caudally to the nervus hyoideus. Between this latter centre of cartilage formation and the hypotrematic process of the first branchial arch a dorsocaudally directed blastema has formed. Caudally, a blastema connects the centre of cartilage formation with the medial side of the ventral part of the first branchial arch. The space between the ventral longitudinal bars in the branchial basket is, caudally, filled up with well developed mesenchyma.

The blastema rostrally to the nervus hyoideus has grown a little further rostrad. Only in its rostral part is any noteworthy development visible. Here the concentration of cells in the medial portion, mentioned in the description of the previous stage, has become still more distinct. In this place the mesenchymatic portion originating from the most dorsal parts of the lateral velar skeleton, adjoins from the medial side. Ventrally, the blastematic portion fuses with the caudal blastema in the place where the latter forms into cartilage.

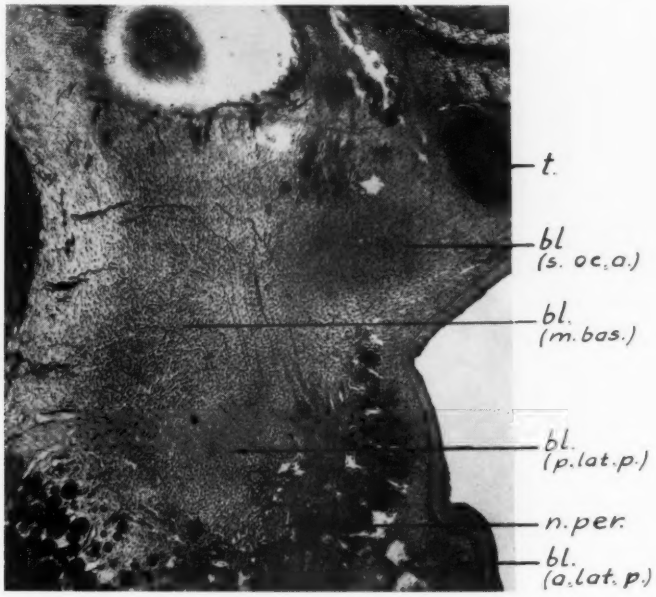

Fig. 36. Metamorphic stage 6. Transversal section through the left part of the head in in front of the eye. 55 ×.

The histological structure of this, especially on the dorsal side rather voluminous, formation is still blastematic. The ventro-caudal part of the blastema has increased in extent, as compared to the preceding stages. It is, in this region, situated between the ventral longitudinal bar and the musculus velothyroideus, a matter to be returned to.

In the subocular portion of blastema procartilage has developed immediately caudally to the rostral ramification of this portion. Rostrally, the branches of the subocular blastematic portion fuse with a blastema in the surrounding mesenchyma (fig. 36). At the place of this fusion two small areas can be distinguished, where the aggregation of cells is more sparse. These areas divide the subocular blastematic portion into three different branches. The dorsal branch fuses with the trabecular commissure, thus corresponding to the identically situated blastema of Stages 4 and 5. However, the ventral branch is now divided in two. The rostral part of the blastematic area extends dorsad from the vicinity of the nervus apicalis. Near the trabecular commissure it fuses with a disc-like blastema which, medially, joins the trabecular commissure. The dorso-lateral portion of this blastematic disc reaches the nervus supraorbitalis (TRETJAKOFF 1927 a), and lies ventrally to the rostral part of the musculus supraocularis (TRETJAKOFF 1926 a).

The portion of the rostral mesenchymatic area on a level with the tentacular

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bases (cf. Stage 4) has developed into a blastema which has some diffuse dorsal connections with the previously described dorsal blastematic portions. In the ventral parts of the mesenchyma a blastema has also begun to develop.

In the larva of Petromyzon the arteria lingualis (Cori 1905—06, Hatta 1922—23) runs latero-ventrally to the muco-cartilage in the ventro-medial longitudinal bar. Rostrally this artery diverges somewhat laterad, and gets into contact with the ventral side of the commissure that unites the basal parts of the lateral mouth plates. Rostrally to this commissure, the artery is rather irregularly ramified. One branch runs to the upper lip, one to the muscles ventrally to the artery (e.g. "releveur, etc.", Damas 1935) and another to the bases of the lateral tentacles. The last-mentioned branch runs dorsad, rostrally to the commissure, and further on the medial side of the muco-cartilage in the lateral mouth plate.

At this stage the relation between the last-mentioned arterial branch and the ventral part of the blastema, formed in the ventral part of the mesenchymatic area, remains identical with that of the muco-cartilage in the ventral larval parts of the lateral mouth plate, as described above. A section through this artery and the ventrally directed branch of ramus maxillaris, referred to in Stage 4, separates the blastematic portion mentioned from the blastema medially to it. This blastema has developed from connective tissue, and is attached to the blastema in the ventro-medial longitudinal bar.

At this stage, the ventral part of blastema has grown rostrad, as is seen from the position of the mesenchymatic area in Stage 4. The caudal limit now lies latero-rostrally to the nerve mentioned in Stage 4, while, previously, the mesenchymatic portion was partly situated straight laterally to it. Immediately caudally to this region lies dissolving tissue, in which blood infiltration has caused small lacunae.

New areas are now being incorporated in the area of blastemas. The blastema begins to surround the sublabial muscles. From here the area of blastemas extends further latero-dorsad, thus invading a region previously occupied by muscles (musculus buccalis superficialis, Tretjakoff 1929 a, Damas 1935).

The blastemas, formed in the medial velar skeleton, in the ventro-medial longitudinal bar and in the nasal capsule, have not notably altered, as compared to the preceding stages.

Some changes are to be observed in the branchial basket. The cartilaginous tips, typical of the branchial basket of the adult, develop as blastematic primordia on each branchial arch. Dorsally to the gill slit, two of these blastematic tips are formed pointing caudad. One of them, the ventral one, situated somewhat dorsally to the rostrally directed part of the epitrematic longitudinal bar developed in the larva, forms the missing part of this bar. The caudal part of the subotic blastema and a small blastematic cushion, situated at the epitrematic part of the loop round the first gill slit, point rostrad on the first branchial

arch. Ventrally to the gill slit, the blastematic connection mentioned above extends from the hypotrematic part of this loop to the anteriorly situated blastema. A blastematic cushion has formed on the ventral curve of the first branchial arch. All these blastematic primordia have indistinct outlines and fuse with rather irregular mesenchymatic streaks, sometimes connecting different blastemas. Similar formations are developed on all branchial arches. Broadly speaking, the adipose tissue in the branchial region has not changed.

Close to the notochord the break in the subchordal longitudinal bar, caudally to the first branchial arch, is gradually filled up with blastema surrounding the tip of the cartilage and formed in the connective tissue round the notochord. Dorso-rostrally the first branchial arch is attached to the parachordal cartilage by means of a tapering cartilaginous bar which increases in thickness, through a formation of cartilage in the connective tissue. In these cases the growth is chiefly appositional.

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g. *Stage 7.* (Diameter of the eye 1700 μ.)

Some of the previously described blastemas have reached their maximal development. This implies that, at the immediately following stage, the blastemas have been reduced or, in any case, have ceased to develop.

The ventral part of the blastema that runs rostrally to the nervus hyoideus is among those that, after this stage, begin to diminish. Fig. 37 shows, in a

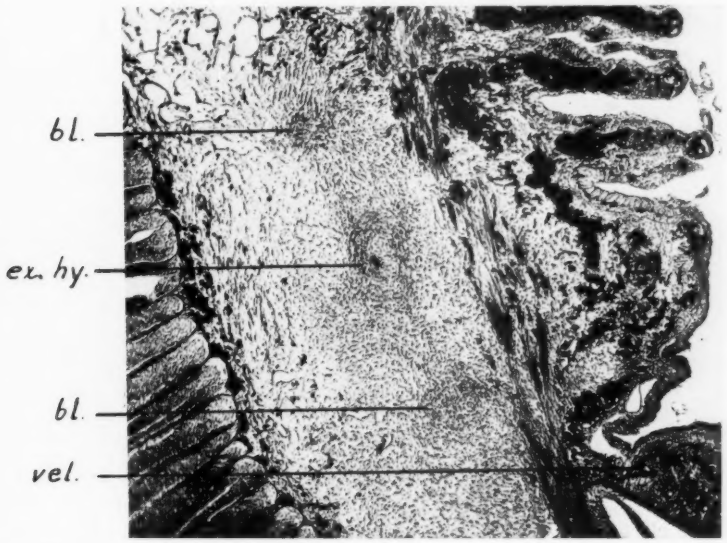


Fig. 37. Metamorphic stage 7. Transversal section through the left body wall showing the ventral blastemas, which caudally fuse with the first branchial arch. 70 ×.

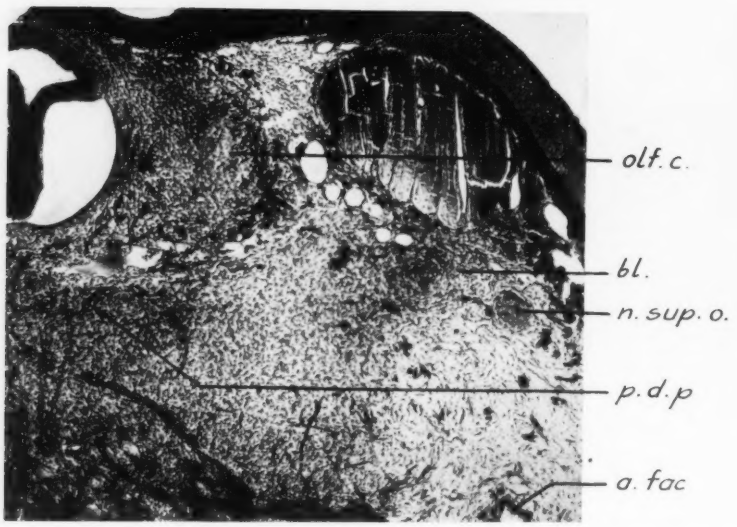


Fig. 38. Metamorphic stage 7. Transversal section through the right part of the head in front of the olfactory capsule. 70 ×.

transverse section, the blastematic connection between the cartilaginous arch round the first gill slit and the blastema (*bl.* at the top) that lies caudally to the nervus hyoideus. Further, this blastema itself is seen (*ex.hy.*), and the maximally developed blastema (*bl.* at the bottom). The particular part of this blastema seen in the figure will diminish and is, later, pushed aside by a muscle blastema. Its dorsal portions, on the other hand, will develop further (cf. the following stage).

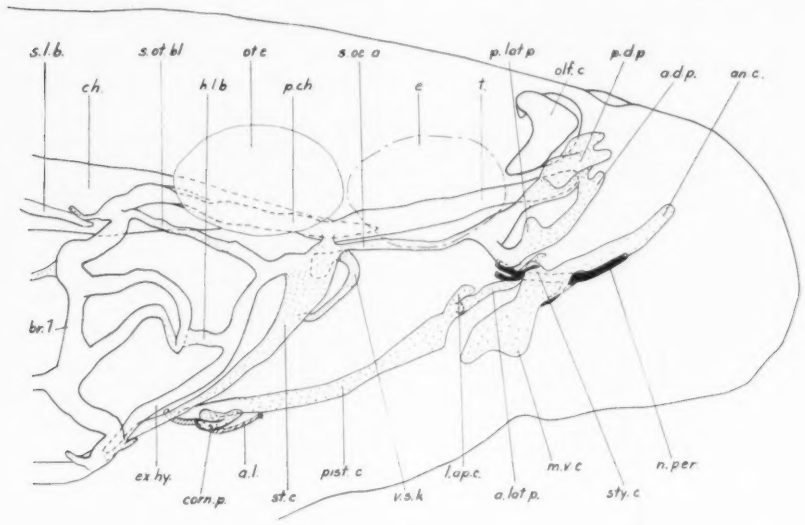
The blastematic portion that lies immediately medially to the nervus supraorbitalis and ventrally to the musculus supraocularis has, likewise, attained its greatest extent (fig. 38). Furthermore, a concentration of cells in this place has resulted in a sort of tissue suggestive of procartilage. Still, the intercellular components are faintly and irregularly developed. It may be remarked here that the degree of development of this blastema—subsequently to be termed the dorso-lateral blastema—seems to vary considerably from one individual to another (cf. later stages).

In the nasal capsule interstitial growth is observed (p. 187).

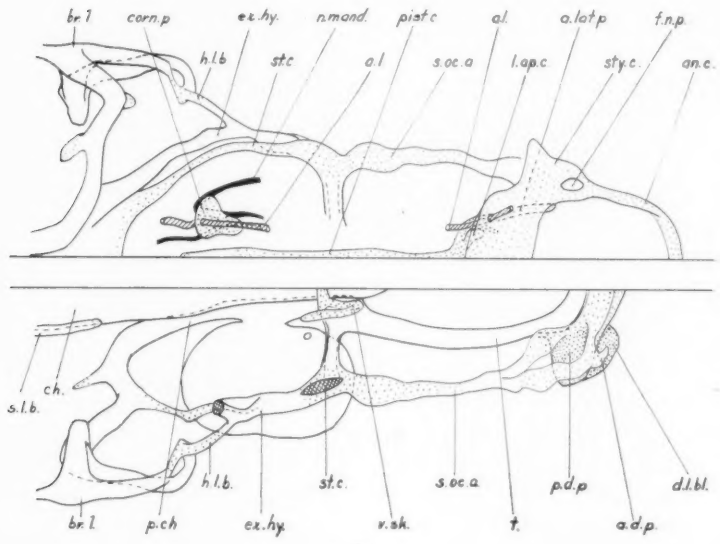
h. *Stage 8.* (Diameter of the eye 1490 μ, cf. reconstruction fig. 39.)

This stage is characterized by a simultaneous appearance of larval and adult organs.

Thus, muco-cartilage still exists in the rostral and medial parts of the ventro-lateral plate, as well as in the rostral part of the rostro-dorsal plate, though



A.



B.

Fig. 39. Metamorphic stage 8. Reconstruction of skull. A. Lateral view, B. Ventral view. Above ventral parts, below dorsal parts.—Dotted area indicates blastema. Cross lines indicate sectioned surfaces. Nerves and vessels as in fig. 26. 15 ×.

the muscular breaking-down processes, described in Stage 6, have advanced. Yet, fragments of muscle bundles are seen even in spots where the dissolution of muscles is far advanced, and primordia of muscle blastemas have already

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appeared while, laterally and rostrally in the upper lip, the buccal musculature remains. Ventrally to the thyroidea, which now shows the first signs of a beginning transformation (cf. KRAENTZEL 1933), the ventral longitudinal bars of the branchial basket are drawing nearer to each another, thus pressing the interlying mesenchymal tissue together. The velum begins to diminish. The area of attachment of the velum at the body wall broadens, indicating that the tissue of the velum moves into the body wall.

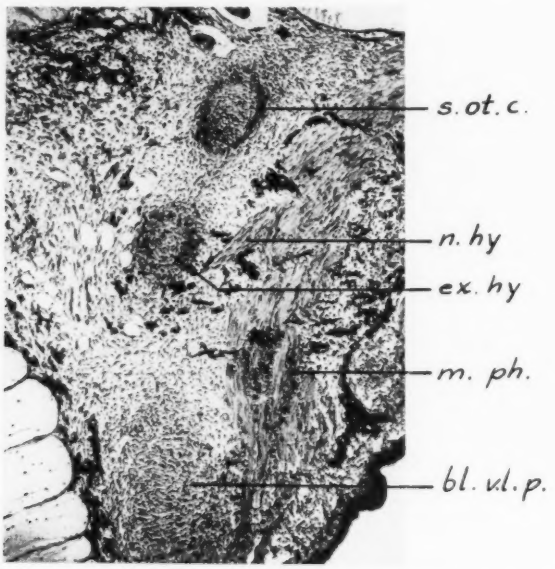

Fig. 40. Metamorphic stage 8. Transversal section through the region at the dorsal part of the extra-hyal. 70 ×.

Owing to comprehensive histological and anatomical differentiations in certain blastemas, primordia of adult skeletal elements have now become easily recognizable. For this reason, the various primordia will, in the descriptions of this and the following stages, be referred to in the same terms as are applied to the corresponding elements in the adult. In the present work the nomenclature used by HOLMGREN and STENSIÖ (1936) and by HOLMGREN (1946) has been adopted. TRETJAKOFF (1926 a, p. 271) has made a compilation of terms used in earlier literature.

The blastema caudally to the nervus hyoideus (TRETJAKOFF 1927 a) has changed entirely into procartilage (fig. 40). It connects the rostral part of the ventral longitudinal bar, at the point where it joins the first branchial arch, with a part of the subotical blastema which also begins to change into cartilage (fig. 40). This procartilaginous element is easily identified with the extra-hyal in the full-grown Petromyzon. Also the blastematic connection with the loop

round the gill slit of the first branchial arch has turned into procartilage. The subotical blastema has changed into procartilage in the part lying closest to the first branchial arch and—as previously mentioned—in the vicinity of the extrahyal. The blastematic portion between these procartilaginous elements has commenced to diminish.

Though histologically not developed to any considerable degree (fig 41), the blastema rostrally to the nervus hyoideus has thickened dorsally. This

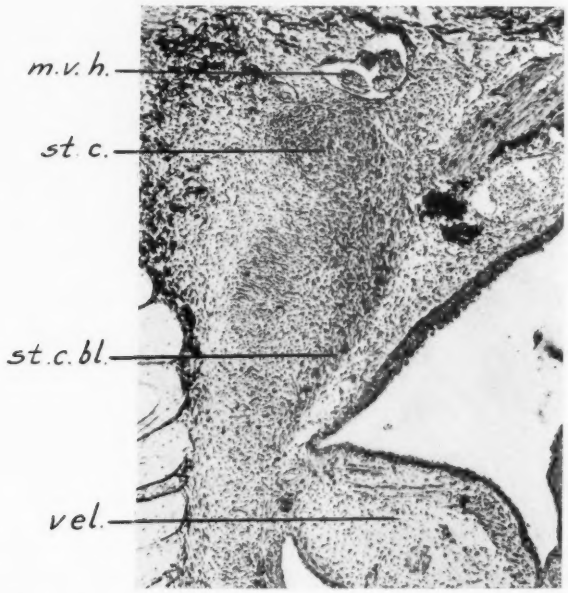

Fig. 41. Metamorphic stage 8. Transversal section through the dorsal part of the primordium of the styliform cartilage. 70 ×.

portion constitutes the primordium of the processus styliformis. Ventrally to this part the blastema has diminished. Medially, another blastema is being formed, viz., a muscle blastema developing from the dissolved pharyngeal musculature situated rostrally to the thyroidea. In later stages the musculus mandibularibranchialis (TRETJAKOFF 1926 a) will form there.

At the point where the nervus mandibulariglossus (TRETJAKOFF 1927 a) branches off from the mandibular portion of the trigeminus, a blastema, of an origin difficult to determine, has developed. It may have formed from dissolved connective tissue previously situated below the epithelium in the cavity of the mouth. Possibly, it has resulted from an immigration of cells from the mesenchyma formed by adjacent muco-cartilage. Or cells from both these sources may have participated in the building up of this blastema. Close to its caudal edge, it is perforated, from the dorsal to the ventral side, by the lingual artery

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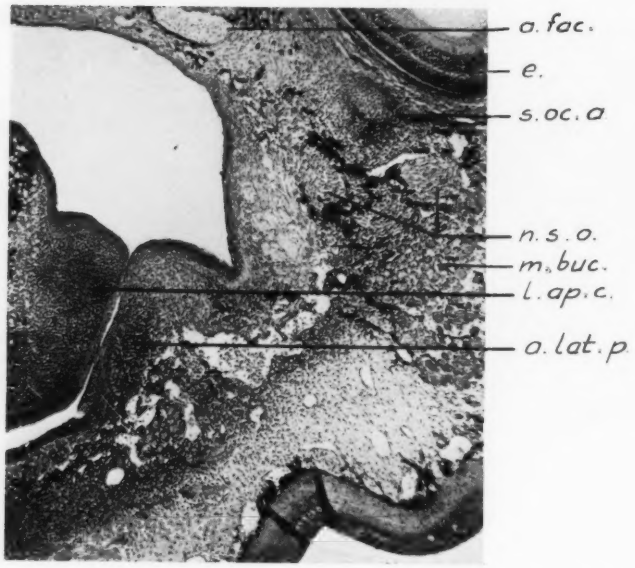

Fig. 42. Metamorphic stage 8. Transversal section through the right part of the head on a level with the anterior part of the eye. 55 ×.

running rostrad, and by the mandibular nerve. It constitutes the first visible primordium of the cornual cartilage which, thus, forms without any contact with the processus styliformis.

The formation of cartilage, mentioned in Stage 6, in the subocular blastema, viz., the primordium of the horizontal part of the subocular arch, has progressed (fig. 42). The caudal parts of the two rostral branches have been transformed into procartilage. The dorsal branch, which forms the primordium of the vertical part of the subocular arch, fuses with the lateral side of the trabecular commissure. Dorsally to the latter, a wing-shaped blastema, medially connected with its vis-à-vis (fig. 43), projects laterad. It forms the primordium of the posterior dorsal cartilage. The dorso-lateral blastema, described in Stage 7, lies medially to the nervus supraorbitalis and ventrally to the rostral part of the musculus supraocularis. At this stage, the blastema (fig. 43) is less developed than in the preceding stage, a condition which is not necessarily due to a reduction. When, in later stages, the histological state in the blastema clearly shows that a reduction has, in fact, taken place, this blastema is often larger than in the present specimen.

The ventro-rostral portion of the subocular blastema has developed further. Its ventral part has changed into procartilage, and represents the connection between the subocular arch and the posterior lateral cartilage. In full-grown animals it is only weakly developed. The primordium of the latter is

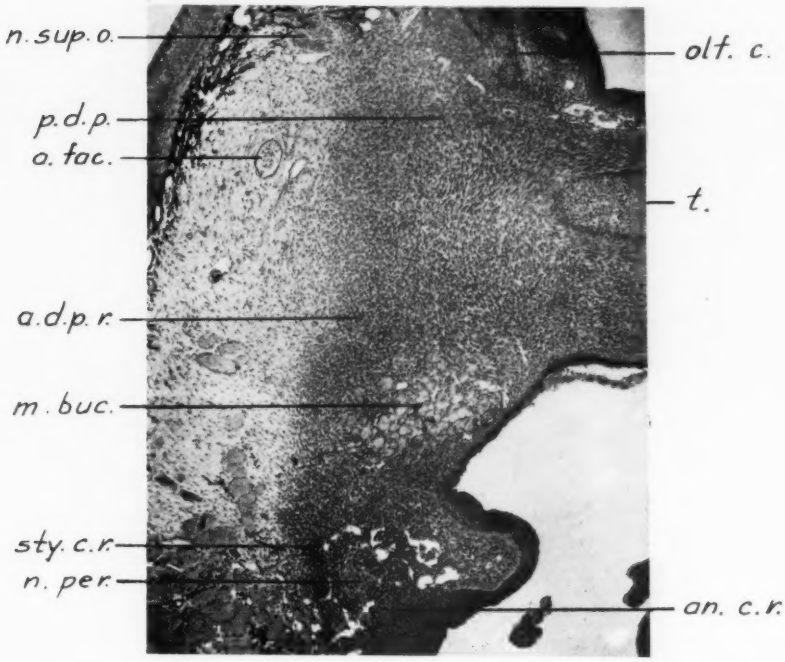

Fig. 43. Metamorphic stage 8. Transversal section through the left part of the head on a level with the trabecular commissure. 55 ×.

found in the dorsal stunt process, immediately rostrally to the place where cartilage is formed. The remaining part of the ventral branch forms the primordium of the anterior dorsal cartilage. Dorso-medially, it is still connected also with the blastema round the trabecular commissure (fig. 43). This connection is slightly reduced, as compared to the preceding stage. Rostrally, the blastema ends in a small process, pointing rostro-mediad. This process is as yet widely separated from its vis-à-vis on the other side. Thus, the primordium of the anterior dorsal cartilage is originally binary.

The blastematic ring round the mouth opening, as described in Stage 6, has now lost its contact with the dorsal blastemas. This ring includes the primordium of the annular cartilage (fig. 43). The perforation for the nervus apicalis (nervus perforans, TRETJAKOFF 1927 a) is easily located. The lateral protuberance, laterally to the nerve, comprises the primordium of the stylet cartilage. Apart from the primordium of the ventral portion of the annular cartilage, the caudo-ventral parts of the blastema contain also the primordium of the medio-ventral cartilage.

When compared to Stage 6, the ventral part of the blastema is seen to have grown further rostrad. The arteria lingualis now ramifies in the caudal part

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of the blastema. The enlargement rostrad seems to be the result of a dissolution of fibres and an increase in the number of cells in the subepithelial connective tissue, on the dorsal surface of the lower lip. At Stage 6, a breaking-down of the caudal parts of the blastema was, as pointed out, observed. Now this process is more lively (fig. 42). A small portion of the base on each side is all that remains of the muco-cartilage in the lateral mouth plates. These portions have the same position as the "abnormal" elements of cartilage at Stage 5. It should be noted that lacunae filled with blood have formed in the tissue elsewhere.

Some changes have occurred in the blastematic complex of the ventromedial longitudinal bar and in the medial tentacle. In its caudal part, situated between the primordia of the cornual cartilages, the elongate blastema that constitutes the primordium of the piston cartilage has changed into procartilage. Rostrally the blastematic knob which carries the rostrally directed pair of processes (fig. 42) is, caudally, by means of a tapering blastema, connected with the primordium of the piston cartilage. It constitutes the primordium of the apical cartilage (TRETJAKOFF 1926 a). The lateral blastematic processes, that extend from this blastema into the lateral wall of the mouth cavity, and project rostrodorsad, form the primordia of the anterior lateral cartilages (fig. 42). The last-mentioned blastemas have developed only slightly.

In the branchial basket and at the junction between the first branchial arch and the parachordal cartilage, the process described in Stage 6 have proceeded but slightly. The connective tissue membrane that closes the fenestra basicranialis, has, in its rostral part, changed into mesenchyma. In the parts of this mesenchyma immediately adjoining to the trabecular commissure, signs of a beginning formation of cartilage are observed. In the nasal capsule, the interstitial growth of cartilage, described in p. 187, is very lively. This kind of interstitial growth has been noticed in five of eight stages which, from the point of view of development, closely approach to each other. In three early stages, of the eight above-mentioned ones, this form of growth was not observed. It should be noted that these zones of growth do not disclose any bilatero-symmetric congruity.

i. *Stage 9.* (Diameter of the eye 1650 μ.)

This stage closely resembles the preceding one. However, the blastema connecting the primordium of the processus styliformis with the ventral part of the extra-hyal, now shows signs of dissolution (fig. 44). The tissue is infiltrated with blood cells. This infiltration is concentrated to the portion of the tissue medially to the ventral parts of the extra-hyal.

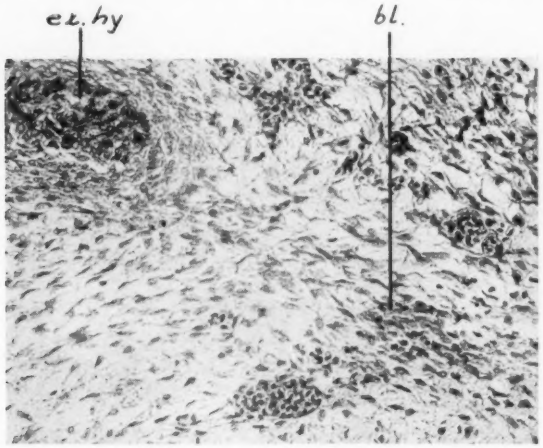

Fig. 44. Metamorphic stage 9. Transversal section through the ventral part of the extra-hyal. Scattered blood cells visible in the blastema (*bl.*) as black points. 290 ×.

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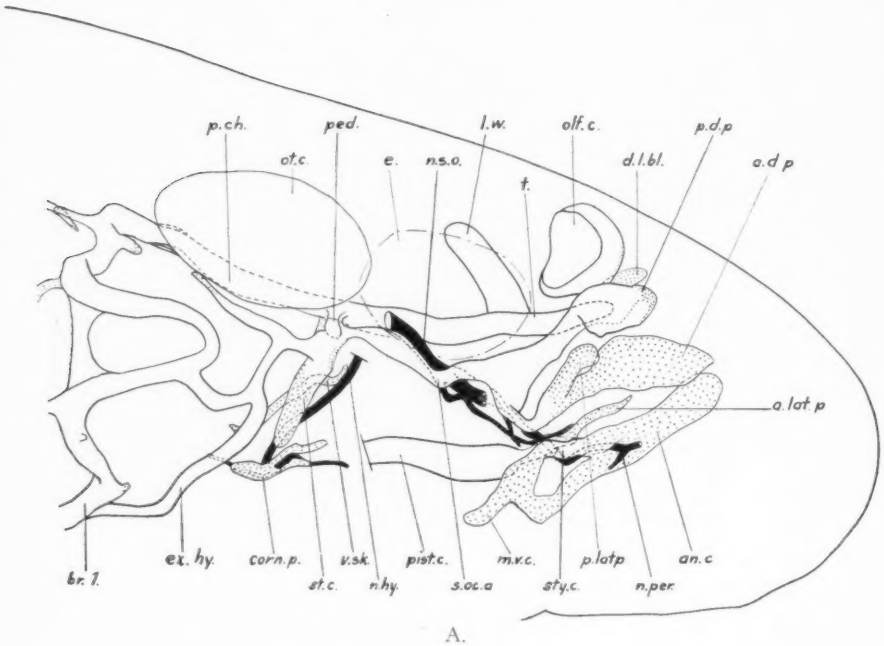
j. *Stage 10.* (Diameter of the eye 1740 μ.)

At Stage 8 a growth in thickness of the lateral walls of the head was discernible. At this stage this thickening process is accentuated. This increase in the thickness of the wall depends largely on changes in the ventro-medial longitudinal bar. As shown in the description of the transformation of muco-cartilage into cartilage (p. 180), the tissue of this structure changes in various ways, entailing a growth in volume. Since, further, this longitudinal bar successively sinks down into the floor of the mouth cavity, a considerable increase in volume follows, extending also laterad, thus affecting the lateral walls.

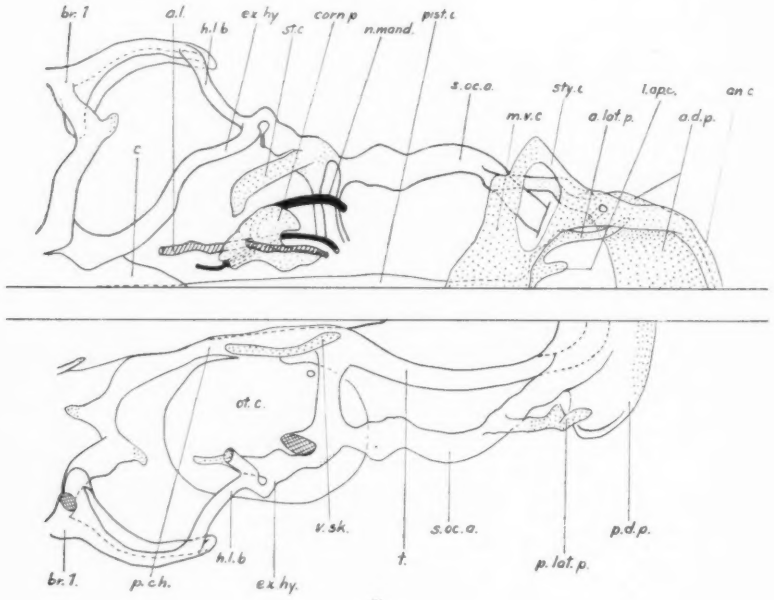
More rostrally in the head, various developing muscle blastemas have the same effect. This applies, in the first place, to the primordium of the musculus basilaris (TRETJAKOFF 1926 a) and the new-formed parts of the subocular musculature. Moreover, part of the tissue of the gradually shrinking velum will, probably, be added to the lateral wall.

k. *Stage 11.* (Diameter of the eye 1780 μ, cf. reconstruction fig. 45.)

At this stage, the muco-cartilage shows signs of destruction everywhere, except, of course, in the primordia originating from it. Thus, small blood lacunae, or isolated blood cells, now appear also in the rostral part of the rostro-dorsal plate and in the medial and rostral portions of the ventro-lateral plate. The ventro-medial longitudinal bar which, as late as at Stage 8, formed a bar projecting into the mouth cavity, is now almost entirely buried in its floor. Only caudally it forms a slight elevation. The lumen of the mouth cavity



A.



B.

Fig. 45. Metamorphic stage 11. Reconstruction of the skull. A. Lateral view, B. Ventral view. Above ventral parts, below dorsal parts.—Dotted area indicates blastema. Cross lines indicate sectioned surfaces. Nerves and vessels as in fig 26. 15 ×.

has considerably diminished, in connection with the growth in thickness of the walls of the head. The velum, diminished in extent, attaches with a broad basal surface to the lateral wall, in which its tissue is partly absorbed.

Around the cartilage in the extra-hyal a perichondrium has formed. The extra-hyal has, thus, assumed the same shape as the caudally situated branchial arches. Caudally, the extra-hyal fuses with the rostral part of the ventral longitudinal bar. Therefore, it does not fuse with the procartilage which fills the space between the longitudinal bars. This tissue continues rostrad, for a bit, in a medially narrowing tip.

The part of the subotical blastema which, at Stage 8, still remained between the procartilaginous portions has now mostly disappeared. In the place, previously occupied by it, mesenchyma is formed which is of the same kind as in other places, filling the area ventrally to the auditory capsule. Apparently, no breaking-down through invasion of any considerable amount of blood vessels has taken place. The remains of the blastema consist of two tips, pointing towards each other, surrounding the ends of the procartilaginous processes. These are situated on the dorsal part of the first branchial arch, and on the horizontal part of the extrahyal, respectively.

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The connection between the cartilaginous loop round the first branchial slit and the extra-hyal has changed into procartilage.

Rostrally, the extra-hyal fuses with a voluminous mass of procartilage (fig. 46), which has developed from the blastema ventrally to the pedicle. The ventral part of this procartilaginous structure has still a blastematic character. It is situated in the medial side of the wall of the mouth cavity (figs. 46, 47). Together, the procartilaginous and the blastematic portions form the primordium of the styliform cartilage which does not, as yet, reach the primordium of the cornual cartilage (fig. 47). Medially and dorsally to these primordia, the velum fuses with the body wall.

The blastematic band which, as late as Stage 8, connected the primordium of the styliform cartilage with the ventral part of the extra-hyal has now completely vanished. The process of dissolution, initiated at Stage 9, has proceeded as far as to extinguish the greater part of the tissues situated next medially to the extra-hyal. An abundance of blood vessels, partly forming lacunae, has here dissolved the blastema, and the surrounding tissue, apart from some small remains.

In a more rostral position, on a level with the primordium of the cornual cartilage, this dissolving process has not spread to the same extent. Here, the blastema mentioned above has been pushed aside by a blastema constituting the first trace of the primordium of the musculus mandibularibranchialis (Tretjakoff 1926 a). Caudally, this latter primordium extends caudo-mediad to the rostrally directed solitary tip which forms the rostral termination of the procartilage portion situated between the ventral longitudinal bars. Evidently, the

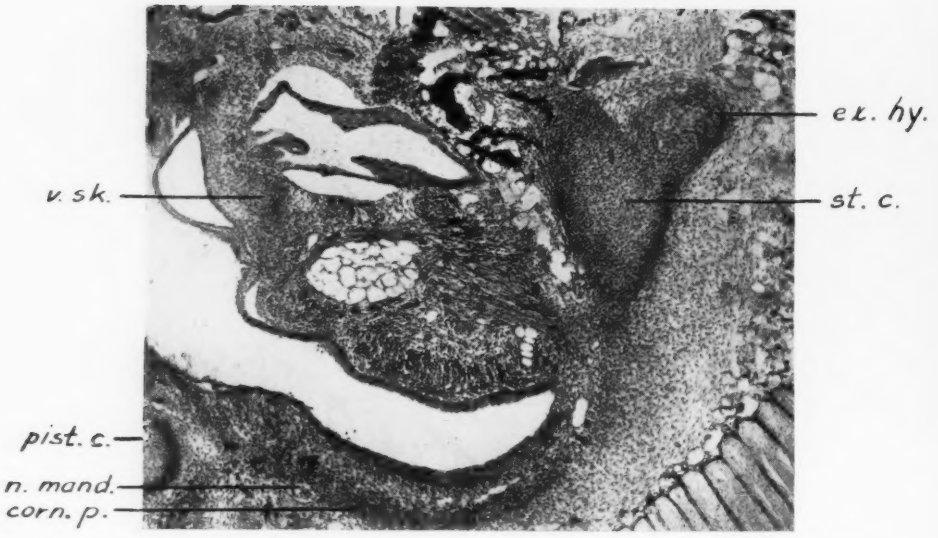

Fig. 46. Metamorphic stage 11. Transversal section through the right body wall showing the rostral part of the extra-hyal and the dorsal part of the styliform cartilage. 55 ×.

muscle blastema has developed from the mesenchyma formed by the dissolved pharyngeal musculature in this area. Medially and rostrally to this muscle blastema lies the primordium of the musculus mandibularis inferior (TRETJAKOFF 1926 a). The first-mentioned muscle blastema has partly the same position as the disappearing blastema situated medially to the extra-hyal. However, these two blastemas have entirely different origins. While the first one is only formed within and by muco-cartilage, the latter one is, as already mentioned, obviously formed by cells from the mesenchyma deriving from the dissolved pharyngeal musculature.

The cornual plate has, on the whole, assumed the same shape as in the adult (fig. 47). It is perforated by the arteria lingualis, as well as by the mandibular nerve, in the same way as in the full-grown animal. Rostrally, two processes project, one medial, and one lateral. The medial one develops between the musculus mandibularis posterior and the musculus mandibulariglossus (TRETJAKOFF 1926 a). The lateral one fuses rostrally with the strongly developed fascia that is developed dorsally to the salivary gland in the musculus basilaris. Caudally, the cornual plate is rounded, and encloses the caudal branch of the nervus mandibularis. The primordium of the cornual plate is still blastematic and has, as stated above, not, as yet, fused with the primordium of the styliform cartilage.

The lateral velar skeleton, which in earlier stages changed into mesenchyma, has now completely disappeared. Evidently, it has been absorbed in the lateral

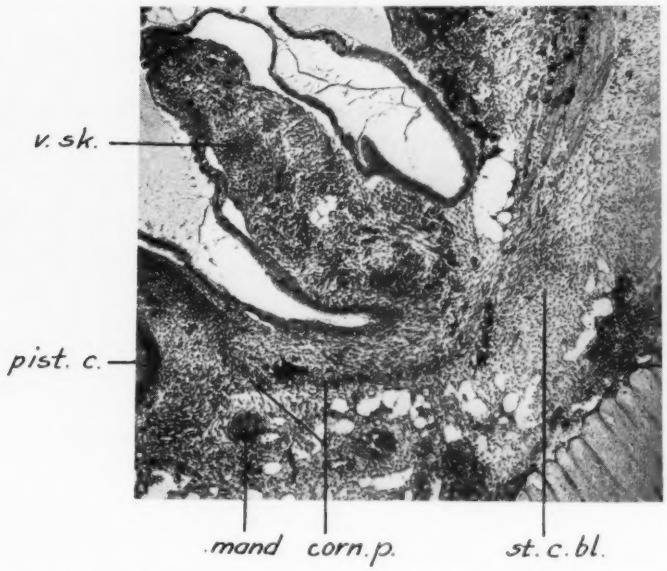

Fig. 47. Metamorphic stage 11. Transversal section through the primordium of the cornual plate. 55 ×.

body wall. It is possible that the mesenchyma mentioned here participates in the formation of the voluminous dorsal part of the styliform cartilage.

The greater part of the subocular arch has now changed into cartilage. At the places of fusion, rostrally to the trabecular commissure and caudally to the pedicle, the tissue is still procartilage.

The blastema around the trabecular commissure has changed into procartilage. The procartilaginous lamella, formed in the rostral parts of the dissolved connective tissue previously closing the fenestra basicranialis, adjoins medially to the trabecle. The lateral and medial parts of the posterior dorsal cartilage have also changed into procartilage (fig. 48). However, the rostral and lateral edges consist of blastema in which numerous cell divisions take place. On the other hand, the dorso-lateral blastema remains and is, in the specimen examined here, weakly developed.

On a level with the rostral part of the eye, an entirely cartilaginous projection issues ventrad from the subocular arch. The blastematic primordium of the posterior lateral cartilage fuses, by means of a procartilaginous part, with this process. The ventral part of this primordium is connected with the blastematic primordium of the anterior dorsal cartilage by means of a rostral process. The anterior dorsal cartilage (fig. 48) has developed, considerably, and fuses in the median line with its vis-à-vis. Though the primordium is still entirely blastematic, it has, on the whole, the same shape as the cartilaginous element in the adult.

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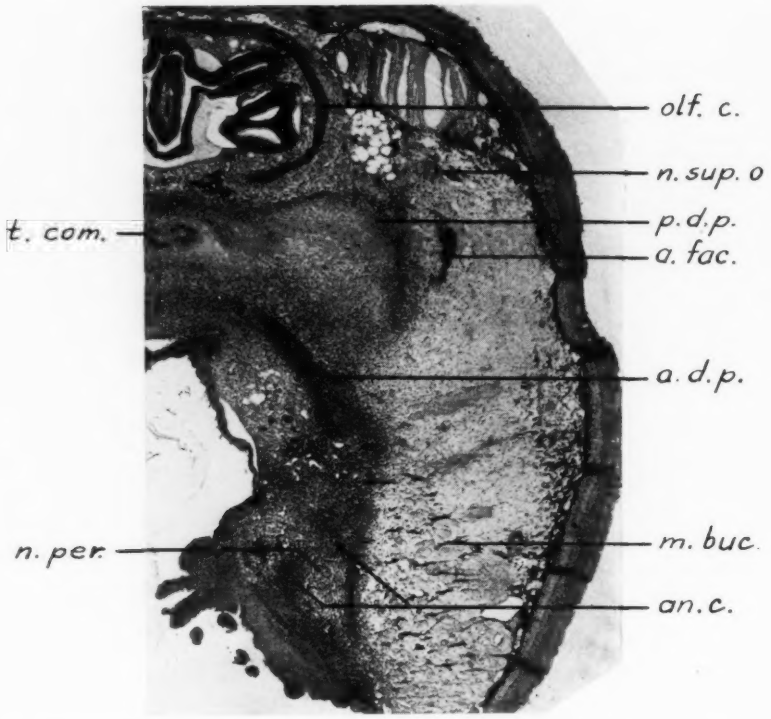

Fig. 48. Metamorphic stage 11. Transversal section through the right part of the head on a level with the anterior part of the nasal capsule. 35 ×.

The tissue between the rostro-dorsal part of the primordium of the posterior lateral cartilage, the caudal part of the anterior dorsal cartilage and the procartilage surrounding the trabecular commissure is characterized by cells of the same type as the blastemas, only slightly more sparse (fig. 48).

The primordium of the annular cartilage has extended but has not changed into cartilage (fig. 48). In a transverse section the dense blastema has the typical, almost triangular, shape characteristic of the fully developed annular cartilage. The ventral portion is less developed. The stylet cartilage is partly cartilaginous. The still blastematic primordium of the medio-ventral cartilage is separated from the ventral portion of the annular blastema by a zone in the previously homogeneous blastema, in which the cells are sparse.

The piston bar consists almost entirely of procartilage (fig. 46). Caudally, however, there is an undifferentiated zone of growth. Rostrally, the still blastematic primordium of the apical cartilage has developed only slightly. The primordium of the anterior lateral cartilage is, also, practically unchanged. The only difference, as compared to earlier stages, is a change in position. While, at the beginning of the metamorphosis, it was situated almost vertically, it has

now changed into a horizontal position. Histologically, there is no development worth mentioning.

In connection with the marked decrease in volume of the velum, the blastema formed in the medial velar skeleton has changed its position. It is now turned caudo-ventrally to the trabecle, instead of rostro-ventrally, as before. It has grown ventrad, while its dorsal parts have diminished (figs. 46, 47).

In the branchial basket only inconsiderable changes are observed. The formation of cartilage which, at earlier stages, started in the various tips, has not been followed by any pronounced development.

The fibrous nasal capsule has, to a great extent, been supplemented with procartilage (fig. 48). Further, medially to the rostral part of the eye, the first signs of cartilage formation in the fibrous cerebral capsule have appeared. The procartilaginous lamella here formed adjoins to the dorsal side of the trabecle, extending from there dorso-caudad.

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1. *Stage 12.* (Diameter of the eye 1700 μ, cf. reconstruction fig. 49.)

This stage is characterized, inter alia, by a pronounced infiltration of blood elements in the mesenchyma between the different organs and primordia of organs. This process of dissolution in the tissue is a step towards the development of exceedingly large venous sinuses, a characteristic feature of the cranial region of the full-grown Petromyzon (LANGERHANS 1873, SCHNEIDER 1879, NESTLER 1890, TRETJAKOFF 1927 b). As will be seen below, the development of these blood lacunae will cause a separation between cartilaginous elements which, during the entire process of formation, have preserved an intimate connection.

The caudo-ventral part of the extra-hyal has moved towards the median line, thus forming a direct continuation rostrad of the ventral longitudinal bar. Ventrally, the peculiar breaking-down phenomena in the cartilage now appear for the first time (cf. p. 224). The main part of the extra-hyal is formed by real cartilage. Procartilage remains only in the connection with processus styliformis, and in the connection caudad with the cartilaginous loop round the first gill slit.

Dorsally, the processus styliformis consists of a voluminous mass of procartilage (fig. 50), which surrounds the rostral, ventral and caudal surfaces of the pedicle. Ventrally the processus styliformis is blastematic, and fuses with the blastematic primordium of the cornual cartilage. This latter has in its caudal part changed into procartilage. The blastematic portion connecting the cornual cartilage and the styliform cartilage consists of longitudinal, as yet fairly sparse, cells (fig. 50). They, thus, differ in shape from the densely lying cells with short processes, usually to be found in the blastematic primordia of cartilaginous elements. This specific shape may, conceivably, be the result of

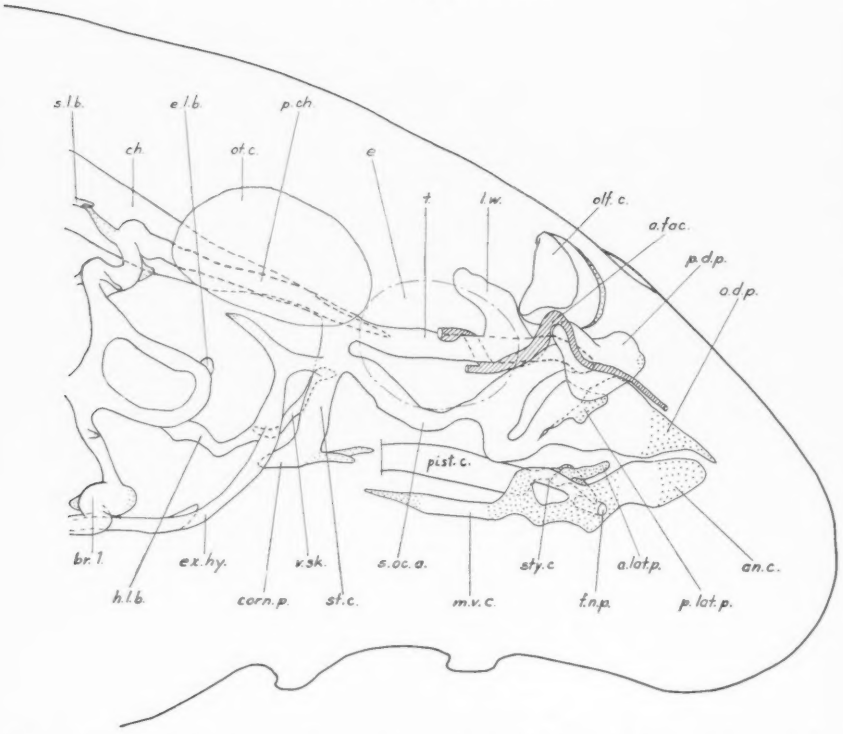

Fig. 49. Metamorphic stage 12. Reconstruction of skull. Lateral view. Dotted area indicates blastema. Blood vessels obliquely striped. 15 ×.

the formation of this blastematic portion which is, wholly or partly, due to an invasion from some other place of cells forming cartilage. The sources of these migrating cells may lie in the lateral parts of the cornual plate, as well as in the dorsal portion of the processus styliformis. The above-mentioned blastema lies in a position previously, it would seem, occupied by the pharyngeal muscles. Medially to it, however, the velum is partly incorporated in the body wall. Laterally to the velum, there is a tissue which probably represents the remainder of the muco-cartilage, previously observed in the velum, and which partly might have contributed to the formation of blastema referred to here.

The subocular arch has now completely changed into cartilage. Its rostral part, i.e. the vertical part of the subocular arch, has moved rostrad. Dorsally, it fuses with the cartilaginous mass round the trabecular commissure (fig. 51) and the cartilaginous portions developed in the rostral part of the fenestra basicranialis. Caudally, the posterior dorsal cartilage, now practically complete, fuses with the cartilage round the trabecular commissure. However, rostrally and laterally, a blastematic zone of growth remains on that cartilage element (fig. 52).

Fig. 50. Transversal section through the left body wall showing the processus styliformis and the primordium of the cornual plate. 55 ×.

The arteria carotis does not run medially but rather, at least partly, dorso-laterally to the trabecle. Rostrally, it runs ventrad, forming the arteria facialis passing the trabecle on the medial and ventral side. From there it continues further rostro-dorsad, laterally to the trabecle, and caudally to the rostral part of the subocular arch. On a level with the caudal part of the posterior dorsal cartilage, it then alters its course rostro-laterad and a little ventrad, thus passing close to the latero-dorsal surface of the posterior dorsal cartilage (fig. 51).

The dorso-lateral blastema, situated medio-ventrally to the nervus supra-orbitalis, is only weakly developed, and reveals no signs of dissolving (fig. 52).

The primordium of the posterior lateral cartilage, the greatest part of which consists of procartilage, with a blastematic zone rostro-dorsally, fuses, caudo-ventrally, with the subocular arch, as was the case in the preceding stage (fig. 51). On the other hand, the connection between this cartilage and the, likewise, cartilaginous anterior dorsal cartilage (fig. 51), is reduced. A piece of procartilage, strongly compressed from the sides, serves as connecting link. Like the rostral part of the subocular arch, both the posterior lateral cartilage and the anterior dorsal cartilage have moved rostrad, which is evident from their changed relations to the trabecular commissure.

The increase in extent of the blood lacunae in the vicinity of the trabecular commissure is the first trace of the dissolving of the blastema that unites the posterior dorsal, the anterior dorsal and the posterior lateral cartilage elements.

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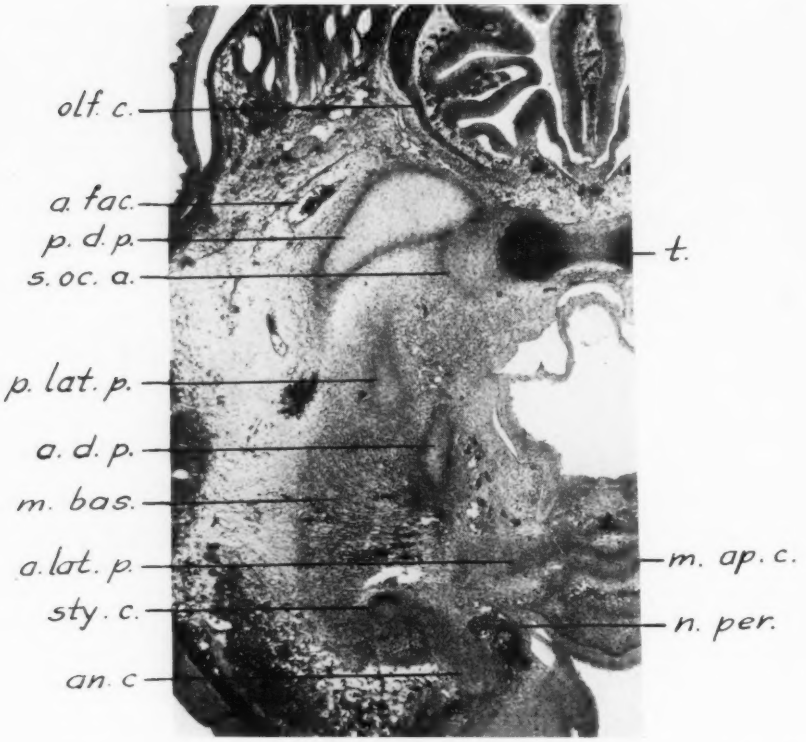

Fig. 51. Metamorphic stage 12. Transversal section through the left part of the head posteriorly to the trabecular commissure. 40 ×.

Dorso-rostrally to the foramen for the nervus perforans, the annular cartilage has changed into procartilage. However, the caudo-ventral part remains, partly, as a blastema (figs. 51, 52). In its caudal part, the medio-ventral cartilage has changed into procartilage. Rostrally to this portion, the laterally directed processes which on each side reach to the caudal ends of the stylet cartilages, are still blastematic. The stylet cartilage has, to a large extent, changed into cartilage (fig. 51).

Ventrally to the eye, the piston cartilage has changed into real cartilage. The other portion consists of procartilage. Caudally, it constitutes a narrow bar, extending caudad past the first branchial arch. A narrow, elongated blastema has formed on each side of the piston cartilage on a level with the cornual cartilage. Rostrally, the connection with the apical cartilage is being reduced.

The primordium of the apical cartilage retains the shape previously described, with two rostral processes. Histologically, the blastema has, however, grown denser, as compared to the preceding stage. The connection with the primordium of the anterior lateral cartilage has become indistinct, simultaneously with a

decrease in extent of this latter primordium (fig. 51). Also here the blastema has become somewhat denser. The velar skeleton (fig. 50) has continued changing into cartilage.

In the fibrous tissue of the nasal and cerebral capsules, the previously described processes continue, though without producing any noteworthy change. In the strong connective tissue, between the parachordal cartilage and the basal parts of the auditory capsule, procartilage has appeared immediately caudally and rostrally to the cartilaginous bar.

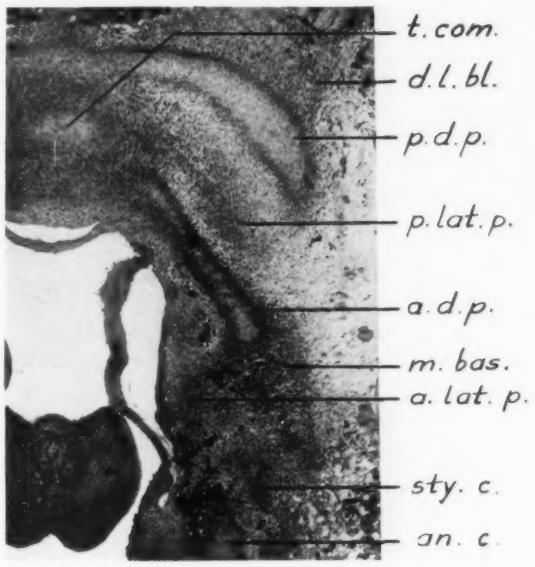

Fig. 52. Metamorphic stage 12. Transversal section through the head anteriorly to the trabecular commissure. 40 ×.

In the branchial basket two small, rostrally directed blastematic tips have developed on every arch, one dorsally to the epitrematic longitudinal bar, and one ventrally to the hypotrematic one. At this stage also a small procartilaginous dorsal pad will be found on the cartilaginous loop round the first gill slit. Otherwise, the conditions in the branchial region resemble previously recorded data.

m. *Stage 13.* (Diameter of the eye 1860 μ, cf. reconstruction fig. 53.)

The dissolving process, initiated at the preceding stage, and resulting in the appearance of blood sinuses, has continued. Big blood lacunae have been formed in various places, separating different organs and primordia from each other. They have, however, not yet acquired the character of fully developed sinuses, since dissolving tissue still remains, often crossing the lacunae as a network consisting of more or less fine meshes. These lacunae are particularly conspicuous in the medio-ventral parts of the ventro-lateral plate, between the extra-hyal and the processus styliformis (fig. 55), and on each side of the strong basilar musculature. In the rostral parts of the head they are less extensive, apart from laterally and caudally to the musculus annularis (fig. 56), where a considerable confluence of blood lacunae is observed.

The extra-hyal has nearly assumed an adult shape. From the point of contact with the cartilage that fills the space between the ventral longitudinal bars, it runs almost laterad. There it turns sharply in a perpendicular direction,

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extending rostrad. After a less sharp, though almost perpendicular, curve, it runs latero-dorsad, fusing with the branch that proceeds from the hypotrematic process of the first branchial arch. Somewhat dorsally to this point the direction is again reversed. After having run a short distance dorso-mediad the "vertical" part of the extra-hyal now described meets the "horizontal" one. Caudally, the latter part terminates in a tip, rostrally it fuses with the processus styliformis.

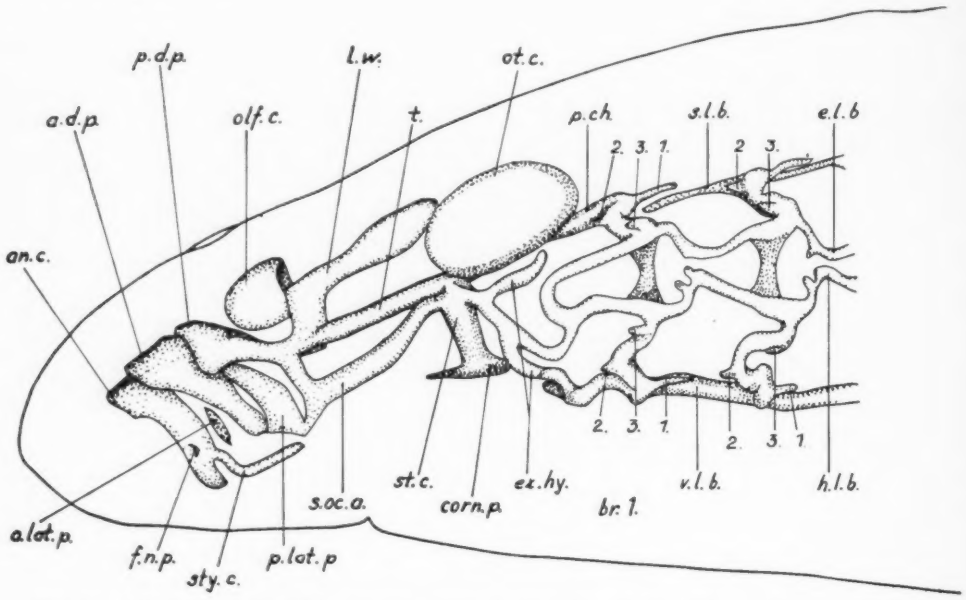

Fig. 53. Metamorphic stage 13. Reconstruction of skull, lateral view. Piston cartilage and medio-ventral cartilage omitted. 12 ×.

The dissolution of the cartilaginous tissue in the ventral parts of the extra-hyal, mentioned in the preceding stage, is now intense. When interstitial growth takes place (p. 187 and fig. 23), the cells of the broken-down cartilage always remain to form mesenchyma and, later, cartilage. In the case of the dissolving extra-hyal tissue, also the cell elements disappear. In principle, the changes in the new-formed cartilage of the extra-hyal signify, rather, a breaking-down process than growth.

As mentioned in the introductory remarks concerning this stage, such processes take place here and there in the tissue, partly in the immediate vicinity of the extra-hyal. In certain cases, a direct communication has opened between the lacunae in the surrounding tissue and the excavations in the extra-hyal. This breaking-down process has been noted in altogether six specimens, at a stage of development approximating to that of Stages 13 and 14. In four of these instances the dissolved areas are large, in two small, though absolutely

distinct. The areas in question are practically always (in five of the six instances), bilateral, and, in addition, symmetric in shape (fig. 54).

Like the cornual plate the greater part of the processus styliformis consists of procartilage. At the point of connection between these structures a small blastematic part remains, where the cells are still of the longitudinal type described in the preceding stage. Furthermore, this part is small.

Dorsally, the processus styliformis is formed like a voluminous mass of procartilage, surrounding the pedicle. The latter, which, in the larva, points

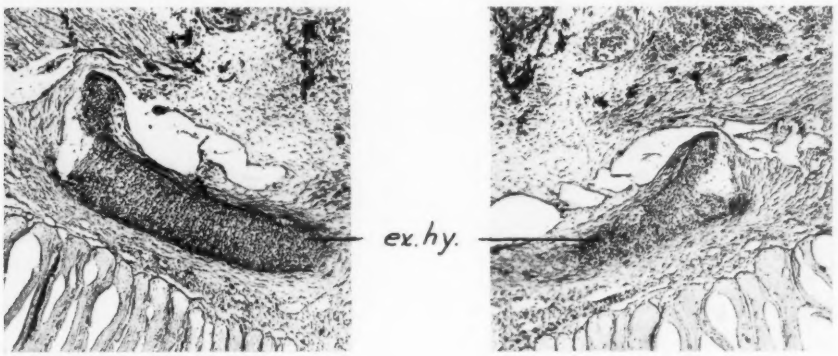

Fig. 54. Metamorphic stage 13. Transversal sections through the ventral parts of the extrahyal on each side. 60 ×.

almost laterad from the trabecle, has now assumed a ventro-lateral direction. From there the processus styliformis passes ventrad in a strongly developed bar.

The cornual plate is perforated in a dorso-ventral direction by the arteria lingualis (fig. 55) which runs rostrad. In the neighbourhood of the centre of the cornual plate the nervus mandibularis ramifies, the posterior branch running caudad through a canal in the procartilage, from which it departs on the caudo-medial side. One branch perforates the plate ventrad, close to the place of ramification (fig. 55), another runs rostrad, dorsally to the cornual plate. The whole complex of cartilage, vessel and nerve seems to have changed its position rostrad, and is now situated almost ventrally to the pedicle. The nervus mandibularis runs medially to the processus styliformis, though considerably closer to it than at previous stages, probably due to the reduction of the velum.

The horizontal part of the subocular arch, runs from the pedicle rostrad, ventrally to the eye. The vertical part, on the other hand, connects the rostral end of the horizontal part with the cartilage round the trabecular commissure. In the rostral part of the fenestra basicranialis the formation of cartilage has proceeded so far that the arteria facialis, on its way rostrad, medially and

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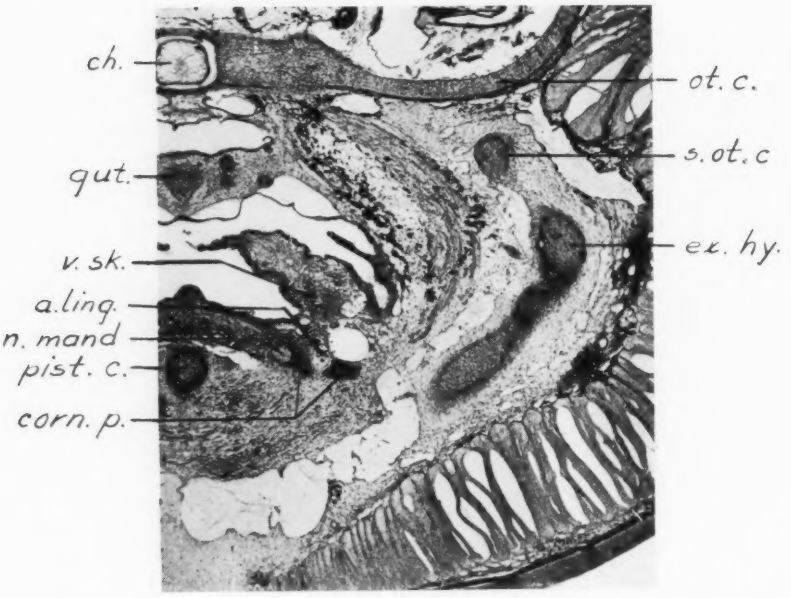

Fig. 55. Metamorphic stage 13. Transversal section through the right body wall on a level with the extra-hyal. 35 ×.

ventrally to the trabecle, is surrounded by cartilage. From there the artery continues dorso-rostrad, caudally to the vertical part of the subocular arch.

Ventro-rostrally a faint connection remains between the subocular arch and the posterior lateral cartilage. The dorsal, still blastematic part of the latter projects between the anterior and posterior dorsal cartilages (fig. 56). The caudal parts of the posterior dorsal cartilage are surrounded by a perichondrium, while, rostrally, a blastematic zone of growth remains which gradually fuses with the surrounding mesenchyma. This area of homogeneous mesenchyma entirely surrounds the different cartilage elements, but is, in their vicinity, slightly infiltrated by blood vessels.

The latero-caudal part of the posterior dorsal cartilage has thickened in the the place of fusion with the basal parts of the dorso-lateral blastema. The dorso-rostral part of this blastema shows signs of reduction. The tissue is not so homogeneous as at previous stages. Blood vessels have developed close to it, laterally and dorsally.

Ventrally the part connecting the anterior dorsal and the posterior lateral cartilage has changed into a small blastema.

The posterior dorsal, the anterior dorsal and the posterior lateral cartilages have now practically assumed an adult shape, the chief difference being that they will later extend more rostrad.

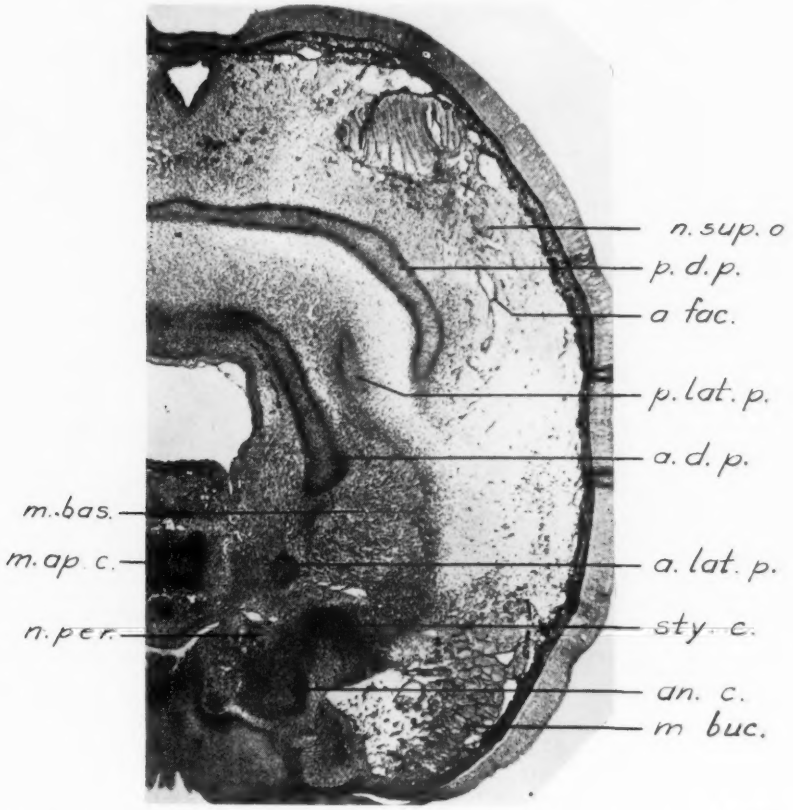

Fig. 56. Metamorphic stage 13. Transversal section through the right part of the head rostrally to the trabecular commissure. 35 ×.

The annular cartilage now consists exclusively of procartilage (fig. 56). Dorsally, the close connection, noticeable at earlier stages, with the rostral part of the anterior dorsal cartilage has been broken, owing to the development of the annular muscle between the two cartilaginous primordia. Ventrally to the foramen for the nervus perforans, the cartilage is less extensive. The stylet cartilage remains closely connected with the annular cartilage.

Also the medio-ventral cartilage has changed into procartilage, assuming, simultaneously, the T-shape characteristic of it in the adult. Laterally, the connection with the stylet cartilage still remains blastematic and decreases in extent. The caudal tip of the medio-ventral cartilage passes, without any distinct delimitation, into the strong fascia that extends in the median line between the muscles, ventrally to the piston cartilage (musculus basilariglossus and musculus copuloglossus, TRETJAKOFF 1926 a).

The stylet cartilage (fig. 56), likewise changing into cartilage, has grown

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caudad. Consequently, it stretches caudally past the place of junction with the lateral process from the medio-ventral cartilage.

The piston cartilage reaches, with its exceedingly thin caudal part, to a level with the second branchial arch. On a level with, and caudally to, the cornual plate, the elongated blastema laterally to the piston cartilage referred to in the preceding stage, has become differentiated. Laterally, it is connected with the blastema of the fascia, situated between the dorsal and ventral half of the musculus mandibularis posterior, which rostrally joins the cornual plate. The transverse section of the piston cartilage is circular (fig. 55), except in the rostral part, where it is oval, with the longer diameter in a dorso-ventral plane.

Rostrally, the piston cartilage fuses with the apical cartilage by means of a narrow procartilaginous portion. The apical cartilage consists of a caudal unpaired plate (fig. 56). Laterally, a small process projects rostrad on each side. The basal part of each one of these tips is perforated, from the lateral to the medial side, by an artery which is a branch of the facial artery, issuing from it ventrally to the trabecle.

The anterior lateral cartilages have lost their connection with the apical cartilage (fig. 56). They are now rather inconsiderable formations on the verge of changing into procartilage in close contact with the mucous membrane.

Though still filled with mesenchyma, the velum now begins to assume the adult shape. Dorsally, a small medial process has developed, into which the dorsal part of the procartilaginous velar skeleton projects. From there the velar skeleton stretches caudo-ventrad and laterad (fig. 55). It ends immediately dorsally to the caudal part of the cornual plate, without having reached it.

The nasal capsule has, exteriorly, assumed its definite schape. The only difference is that the tissue partly remains as procartilage. The medial wall is only indicated, by a blastema in the still largely intact connective tissue.

On the lateral side of the fibrous cerebral capsule the cartilage formation has extended caudad, reaching the rostro-medial side of the auditory capsule. The prootic cerebral nerves, except the facial and olfactory nerves, leave the cerebral cavity through the area surrounded by this lateral cartilage, by the trabecle and by the auditory capsule.

The auditory capsule has become connected with the parachordal cartilage by means of procartilage developed in the connective tissue previously situated here.

There are six small processes on each branchial arch. Three are situated dorsally to the epitrematic longitudinal bar and three ventrally to the hypotrematic longitudinal bar. The topmost and the undermost of the six processes are directed caudad and will be referred to as No. 1, the remaining four project rostrad. The two processes immediately above the epitrematic longitudinal bar and underneath the hypotrematic longitudinal bar will be called No. 3 and the remaining two No. 2 (see fig. 53).

The epitrematic longitudinal bar is now completed. The subchordal longitudinal bar has grown rostrad, though without getting as far as the first branchial arch. The space between the ventral longitudinal bars has diminished and is now occupied by a thin cartilaginous lamella. It has no connection with the ventral longitudinal bar in the places where the branchial arches issue. It recalls the conditions in the larva where there was no connection between the ventral longitudinal bar and the muco-cartilage in these places. Rostrally, this ventro-medial cartilage lamella, in the specimen examined here, terminates in two rostrally directed tips.

The cartilaginous rings round the gill slits, characteristic of the fullgrown animal, have developed as blastemas. These blastemas are formed from the fibrous connective tissue which is situated in the corresponding place in the larva.

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n. *Stage 14.* (Spawned animal, cf. reconstruction fig. 57.)

Only fractions of the mesenchymatic portions that remained at Stage 13 are left in the full-grown specimen. These fractions have changed into loose connective tissue. This tissue is quite sparse, being noted in larger accumulations only ventrally to the cartilaginous auditory capsule and round the collagenous orbit. The layer of loose connective tissue which is situated under

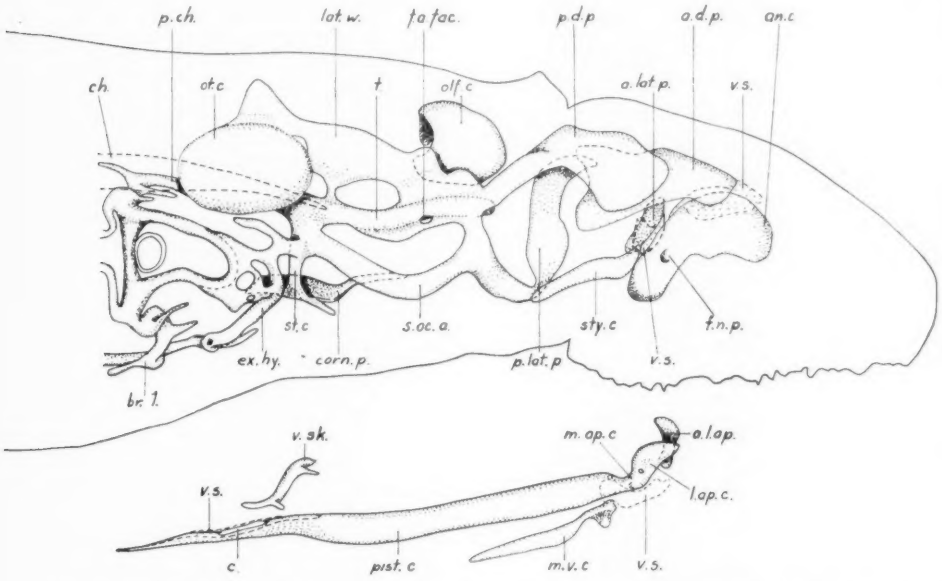

Fig. 57. Metamorphic stage 14. Reconstruction of skull of adult, lateral view. The ventral elements shown separately. Vesicular supporting tissue (*v.s.*) indicated by broken lines. 10 ×.

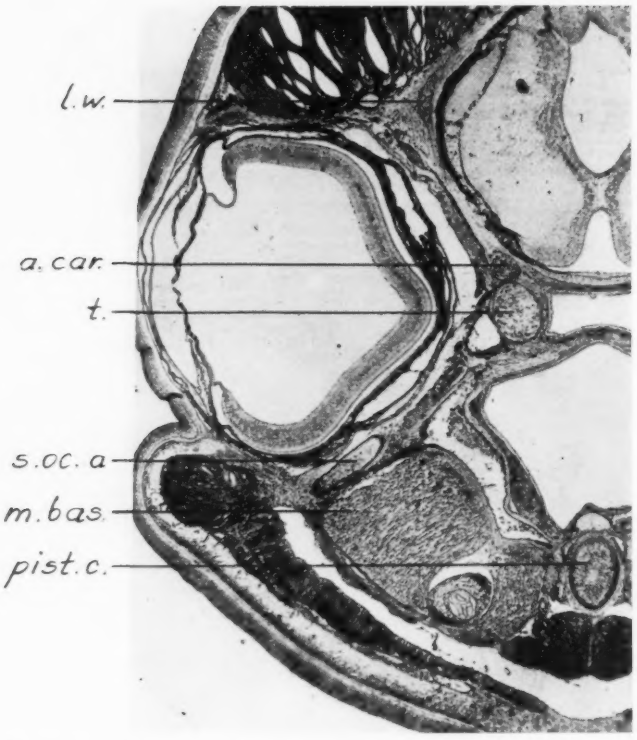

Fig. 58. Metamorphic stage between 13 and 14. Transversal section of the left part of the head on a level with the anterior part of the eye. 35 ×.

the aponeurosis of the chorium in the full-grown animal has developed in a specific manner and has nothing to do with the mesenchyma inside the corium of the larva. The larval aponeurosis is divided into an outer and inner lamella because of the dissolution of collagenous fibres in the middle layer. The free cells in this layer form loose connective tissue. In addition, a stratum with densely collected cells is formed on the inside of the outer lamella. It is the seat of proliferous cell divisions. Medially to this loose connective tissue, a layer of the original connective tissue remains. It is, thus, a descendant of the inner parts of the larval aponeurosis.

The sparse occurrence of loose connective tissue in the full-grown animal is, apparently, due to the development of the previously mentioned venous sinuses. At a stage, immediately subsequent to Stage 13 (fig. 58), the various blood lacunae have already coalesced into sinus-like formations, the walls of which are, at least partly, covered by regular endothelium. In the fully developed specimen (fig. 59) this process has gone so far that nerves and blood vessels often run through such blood lacunae, surrounded only by a thin layer of

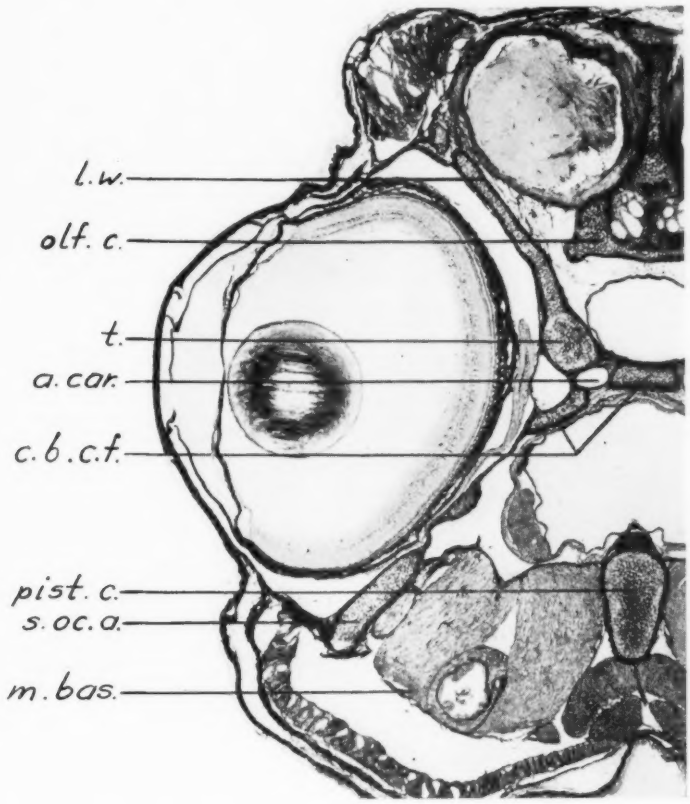

Fig. 59. Metamorphic stage 14. Transversal section through the left part of the head on a level with the rostral part of the eye. 35 ×.

connective tissue and endothelium. These sinusal formations will separate not only muscles from each other, but also certain cartilaginous elements, for instance, those in the rostral part of the cranium.

The rostral, buccal musculature of the larva remains for a considerable time after Stage 13 but, in the mature Petromyzon, it has disappeared. Its dissolution takes place successively. Simultaneously, the annular musculature increases in volume.

The branchial muscles do not seem to be subjected to any considerable changes in the course of the metamorphosis. According to SCHNEIDER (1879) and BUJOR (1890—92), no musculature, of the specific type described, first, by STANNIUS (1851), is to be found in the full-grown animal of Petromyzon fluviatilis. This type of musculature is characterized by the fact that the myofibrils develop only in the periphery of a muscle fibre. In later metamorphic stages (12 and 13), an infiltration of blood cells can be detected in

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this musculature, while such an infiltration never takes place in the normal branchial musculature. It seems likely that changes of some kind arise in this connection, but no dissolution of the tissue has been observed. As NESTLER (1890) points out, the difference between the two types of muscles remains, in the branchial region of Petromyzon planeri, after metamorphosis. However, it would be outside the scope of the present investigation to dwell more closely on this subject.

The shape of the extra-hyal is, at this stage, virtually the same as at Stage 13. However, the connection between the extra-hyal and the cartilaginous loop round the first gill slit has, in this particular specimen, a peculiar formation (fig. 60). Though in no way normal, the matter deserves some attention. Ventrally, the usual connecting bar can be distinguished, but, dorsally to it, an additional pair of cartilaginous bars have developed, the dorsal one directly attaching to the extra-hyal. Apart from these exceptional details, the extra-hyal is normal.

Neither the processus styliformis nor the cornual cartilage seem, from a morphological point of view, to have changed notably as compared to the previous stage. Histologically, the cartilaginous tissue is, however, more differentiated. In this specimen the lingual artery and the ventral branch of the mandibular nerve pass through one single foramen in the cornual plate.

The vertical part of the subocular arch has, ventrally, a rostrally directed process, which serves as a connection with the posterior lateral cartilage. Like the anterior and posterior dorsal cartilage, the annular cartilage and the anterior lateral cartilage, this latter cartilage has moved, considerably, rostrad, as compared to Stage 13, as has also the medio-ventral cartilage. The histological differentiation has advanced but, morphologically, no noteworthy changes have taken place.

Also the piston cartilage has the same shape as at the preceding stage. The blastema that was situated laterally to the piston cartilage, on a level with, and caudally to, the caudal part of the cornual plate, has partly changed into a thin cartilaginous bar. The piston cartilage is in a transverse section triangular in this part (fig. 60).

The apical cartilage fuses rostrally with the piston cartilage by means of a narrow piece of "soft" cartilage. It consists of a medial plate, from each side of which the rostrally directed processes project. Dorsally and medially to the latter are two small, free cartilage elements, viz., the anterior apical cartilages, which have their origin in the connective tissue immediately underneath the epithelium.

Soon after Stage 13, the binary primordium of the velar skeleton meets dorsally in the two medially directed processes on the velar apparatus, mentioned in the preceding stage, ventrally to the place where the oesophageal aperture

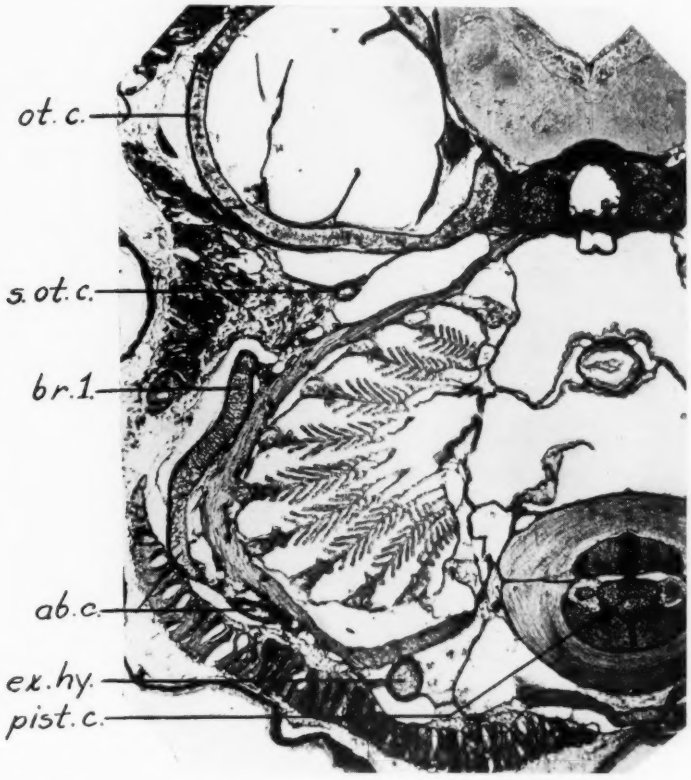

Fig. 60. Metamorphic stage 14. Transversal section through the left body wall in front of the cartilaginous loop round the first gill slit. 35 ×

forms. Rostrally directed cartilaginous processes supporting the velar tentacles are formed in this region. Ventrally, the velar skeleton ends on each side in a small cartilaginous plate which carries a small process pointing rostro-laterad. This process gets into a close contact with the caudo-medial part of the cornual plate but no fusion takes place. Another tip points caudad.

In the nasal capsule a cartilaginous lamella has developed in the caudo-medial wall (fig. 59). The cartilaginous lamella in the lateral wall of the cerebral capsule has grown caudad, along the dorso-medial wall of the auditory capsule. Dorsally, it terminates in an incomplete tectum synoticum which is formed dorso-medially to the middle part of the auditory capsules. This tectum is more or less complete in different specimens. Close to the auditory capsule, two fenestrae have formed in the cartilaginous lateral wall. The dorsal one does not serve as a passage to any nerve, while the root of the nervus trigeminus runs through the ventral one. Rostrally to this is the so-called opticus fenestra, through which the three eye-muscle nerves and the nervus opticus run.

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In the adult animal the fenestra basicranialis anterior differs in shape from that in the larva. The laterally curved trabecles are straightened out, running practically parallel to each other. The space between them has diminished. A cartilage lamella originating from the cartilage that at the preceding stage was forming rostrally between the trabecles now fills up more than the rostral half of the cranial fenestra. This lamella is penetrated on each side by the foramina for the arteria facialis. This artery penetrates also the sharp edges which have formed ventrally to the trabecles.

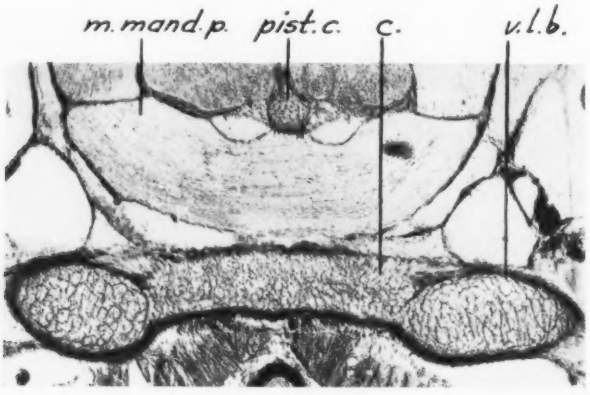

Fig. 61. Metamorphic stage 14. Transversal section through the ventral longitudinal bars between the first and the second branchial arch. 200 ×.

The connective tissue round the notochord has changed into cartilage caudally to the tip projecting into the fenestra basicranialis. This process is slightly more advanced on the dorsal side than on the ventral.

The branchial region has not altered much from previous stages. Cartilage has begun to form in the ring-shaped blastemas round the gill slits, described in the preceding stage. The processes on the branchial arches have all grown into practically the same size. Histologically, the differentiation has not gone far. The intercellular substance is weakly developed.

The cartilage formed during the metamorphosis reveals varying degrees of development. In certain places the matrix is weakly developed. This applies, as stated, to the cartilage in the branchial region, as well as to the peripheral parts of the posterior dorsal plate, to the rostro-dorsal part of the posterior lateral cartilage, to the entirely cartilaginous complex in connection with the extra-hyal, and, finally, to the cartilage plate situated between the ventral longitudinal bars (fig 61). Otherwise, for instance in the subocular arch, the processus styliformis, the cornual plate, the annular cartilage and the middle parts of the anterior and posterior dorsal cartilages, the intercellular substance is better developed. In certain instances, e.g., between the apical and piston cartilages, as well as between the processus styliformis and the cornual plate,

two well developed cartilaginous portions are connected by a piece of "soft" cartilage.

STUDNIČKA (1897) refers to a specific kind of connective tissue which he calls "parenchymknorpel". He found this tissue, by SCHAFFER (1903) termed vesicular supporting tissue or "chondroides Stützgewebe" (1930), on the edges of the rostral cartilages and under the rostral part of the lingual cartilage. The distribution of this vesiculous connective tissue in a full-grown animal can be seen from fig. 57 (*v.s.*). These parts develop from blastemas, which in no way differ from the cartilage-forming blastemas with which they, as a rule, fuse without any boundary line.

3. SUMMARY OF THE PROCESS OF METAMORPHOSIS.

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In the sparse literature dealing with the metamorphosis information of a very contradictory nature is often met with. Concerning the histological side of the matter this fact has already been stated. Literary data will be discussed below. At the same time a summary of the most significant results from the preceding description of stages will be given.

As mentioned, the extra-hyal is found to originate, partly within and from muco-cartilage, on the edge of the ventro-lateral plate that runs rostro-dorsally from the first branchial arch, partly outside the area in which muco-cartilage is distributed. This latter part of the extra-hyal is situated immediately caudally to the place, where the nervus hyoideus, running ventro-caudad, passes the extra-hyal from the medial to the lateral side. In the larva the muco-cartilage never extends caudally to this nerve (fig. 5). TRETJAKOFF (1929 a) definitely denies that cartilage is derived from muco-cartilage. In his view—which, however, seems to be exclusively based on observations of late metamorphic stages—the extra-hyal develops medially to the muco-cartilage of the ventro-lateral plate, having, therefore, nothing to do with the latter. This opinion is shared by DE BEER (1937). On the other hand, practically all other authors, who have dealt with these problems, have brought forth facts refuting this interpretation (NESTLER 1890, BUJOR 1890—92, SCHAFFER 1896, BALABAI 1935, DAMAS 1935, HOLMGREN och STENSIÖ 1936). They are of the opinion that the extra-hyal is developed from muco-cartilage in the caudo-dorsal edge of ventro-lateral plate. To some extent, BALABAI has a different opinion. He suggests that the processus styliformis and the cornual plate ("cartilago mandibularis"), as well as the extra-hyal ("cartilago hyoideum"), have their origin from the muco-cartilaginous portion that he calls the "subauraler Ammocoetesbogen". He seems, however, to have overlooked that the existence of the nervus hyoideus, even at early stages, renders distinctions between the primordia of these two structures possible, at least in the dorsal region. Ventrally, the closely situated blastemas defy any definitions at early stages.

Similarly, the other authors have, apparently, failed to observe that the nervus hyoideus runs rostrally to the extra-hyal but caudally to the ventro-lateral plate. In fact, for this very reason, the entire extra-hyal cannot have been formed in the muco-cartilage within the ventro-lateral plate.

As regards the processus styliformis and the cornual plate, the process of development is more complicated. KAENSCHE (1890) maintained that these elements are formed in the muco-cartilage of the ventro-lateral plate. BUJOR (1890—92), on the other hand, stated that they "prennent naissance dans le tissu conjonctif régénéré du velum", i.e. (provided that he has been correctly interpreted by the present author) in the muco-cartilage of the lateral velar skeleton. SCHAFFER (1896) in the main adopted KAENSCHE's opinion, while TRETJAKOFF (1929 a) referred to the development of the "mandibular arch" as a satisfactory proof of his interpretation that muco-cartilage can not be transformed into cartilage. Instead, he suggested, as in the case of the "hyoid arch", the simultaneous existence of a muco-cartilaginous and a cartilaginous arch. According to DAMAS (1935), the processus styliformis originates "dans la sangle ventrale, le long de l'insertion du vélum", while the cornual cartilage would arise, in a different way, "dans le tissu conjonctif sous le vélum". As stated in connection with the description of the origin of the extra-hyal, BALABAI (1935) held the view that the "cartilago mandibularis" develops from the same primordium as the extra-hyal. He does not mention any special observations concerning the cornual cartilage, nor has he, it would seem, noticed the existence of the pedicle in the larva. He is of the opinion that a special process on the "subaural" arch dorsally fuses with the trabecle. A division of the "subaural" arch would, he states, take place ventrally to this place of fusion, though comprising but the dorsal part of the arch. The rostral part of the "subaural" arch, thus formed, constitutes the primordium of the "cartilago mandibularis". Together with the e n t i r e ventral part of the "subaural" arch, the caudal branches (cf. BALABAI 1935, figs. 17—22), fusing with a process developing from the rostral loop of the first branchial arch, should form the extra-hyal. On account of the considerable developmental gap between BALABAI's last metamorphic stage and the full-grown animal, the final differentiation of the various parts of the "cartilago mandibularis" is difficult to understand. HOLMGREN and STENSIÖ (1936) express the opinion that the processus styliformis, as well as the cornual plate, develop from the muco-cartilage of the ventro-lateral plate.

The development of the processus styliformis and the cornual cartilage is far more prolonged in time than that of most other cartilaginous elements. Different stages can be distinguished in this process. The first stage results in the formation of the common blastematic primordium of the processus styliformis and the extra-hyal. This stage agrees well with the three first stages represented in BALABAI's drawings. At the next stage the extra-hyal changes

into procartilage, while the primordium of the processus styliformis changes its position, mediad in the lateral wall of the head. Ventrally, this blastema breaks down. At the third stage, the dissolving process results in an attack also on the new-formed cartilaginous tissue in the extra-hyal. In this phase, the processus styliformis has gradually changed into procartilage. Eventually it reaches the primordium of the cornual cartilage which also changes into cartilage. At these late developmental stages, the position of the processus styliformis, may, on one hand, make BUJOR's conclusion understandable, viz., that tissue from the velum should play a predominant part in its formation, an opinion which will not be altogether rejected in the present investigation, and, on the other, be a precedent for TRETJAKOFF's views. TRETJAKOFF states that, during the whole of this process, muco-cartilage lies laterally to the primordium of the styliform cartilage. Laterally to the primordium, portions of tissue, derived from muco-cartilage, will, no doubt, remain. Obviously, these differences of opinion are to be explained from the fact that an insufficient number of metamorphic specimens have been at the disposal of the authors. Only a minute study of closely consecutive developmental stages can produce the necessary facts for the understanding of the complicated origin of the styliform cartilage.

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The first traces of the blastema of the processus styliformis, rostrally to the nervus hyoideus, originate exclusively from muco-cartilage. While the cells are concentrating towards the medial side of the body wall, the fibres of the connective tissue underneath the mucous membrane dissolve. Afterwards, the cells thus freed participate in the formation of the blastema. Meanwhile, also the velum is reduced in size. There is, presumably, nothing that contradicts the possibility that the connective tissue of the velum also contributes to the formation of the blastema. Laterally, rests of muco-cartilage, not absorbed by the blastema, remain even at late stages (12, 13).

The cartilage forming of the processus styliformis begins in the region of the pedicle which is, then, surrounded by procartilage. Then the process grows ventrad. The last part changed into cartilage is the connection with the cornual plate.

As DAMAS (1935) has pointed out, the cornual cartilage originates in the connective tissue ventrally to the velum. In the Ammocoetes larva, there is no visible difference between the part in which the cornual plate develops and the parts situated caudally and rostrally to it. For this reason, it is difficult to define the part from which this cellular material is derived. The difficulty is increased because of the fact that other metamorphic processes occur in the same place. Anyhow the cornual cartilage is formed without any primary connection with the processus styliformis. Rostrally and caudally, muscle fascias fuse with the cartilage of the cornual plate, as stated in the descriptions

of stages above. The relation between the cornual cartilage and the medially situated piston cartilage will be dealt with below.

The different parts of the subocular arch develop from different sources. The cartilage caudally adjoining to the pedicle process no doubt originates from muco-cartilage. The cartilage ventrally to the eye is formed in the fibrous tissue, to be found there in the larva, while, rostrally, the situation is more complicated. As shown in the descriptions of stages, a portion of the subocular muco-cartilage and the muco-cartilage fused with the trabecular commissure have taken part in the formation of the blastema, while the area between these portions in the larva is occupied by the dorsal parts of the musculus depressor labii superioris. This muscle must be dissolved before a contact can be established between the forementioned portions of the blastema.

KAENSCHE (1890) considered that the subocular arch in the full-grown animal had formed in the muco-cartilage of the dorsal rim of the ventro-lateral plate. BUJOR (1890—92) is of the opinion that it originates in the "jeune tissu conjonctif" developed in the part situated ventrally to the eye. BALABAI (1935) suggested that the muco-cartilage, ventrally and rostrally to the auditory capsule, was the source of its origin. The cartilage was, in his view, first developed in this region, and then extended rostrad. DAMAS (1935) states that the subocular arch arises from "le tissu conjonctif de néoformation". According to HOLMGREN and STENSIÖ (1936), the subocular arch develops in a muco-cartilaginous plate "unterhalb der Spitze des ventralen segmentierten Muskulatur". The pedicle is supposed to have no primary connection with the subocular arch. It is, further, stated that the particular part of the primordium of the subocular arch "der an den Seitenteilen der Vorderpartie des Trabekel anstösst" is penetrated by the arteria facialis. However, as is seen from the descriptions of stages, the arteria facialis always runs caudally to the subocular arch. In the full-grown animal, this artery penetrates the ventrally directed cartilaginous lamella, adjacent to the ventral surface of the trabecle.

SCHNEIDER (1879) supposed that the posterior dorsal cartilage ("Ethmoid") was formed from the muco-cartilage of the rostro-dorsal plate. KAENSCHE (1890) considered that the annular cartilage, the anterior dorsal cartilage and the posterior lateral cartilage had the same origin. BUJOR (1890—92) also was of the opinion that all "les cartilages labiaux" developed in this manner, adding that "les jeunes cellules cartilagineuses ont aussi la même constitution et la même forme". According to SCHAFFER (1896), the posterior dorsal cartilage and the dorsal part of the annular cartilage are derived from muco-cartilage in the rostro-dorsal plate. On the other hand, the ventral part of the annular cartilage was supposed to originate in the rostral part of the ventro-lateral plate. It is possible that SCHAFFER's intention was to ascribe the origin of the cartilage elements situated between the two forementioned structures to the same portion of muco-cartilage, though he does not definitely say so. In the

opinion of TRETJAKOFF (1929a), the muco-cartilage in the rostro-dorsal plate had nothing to do with the development of any cartilage.

BALABAI (1935) assorts the rostral cartilage elements into one group ("cart annularis, lateralis, rhomboidea, tectoria, trabecularis, spinosa" and the vertical part of the subocular arch, including also the piston and apical cartilages). As regards their origin, he gives no direct information, apart from suggesting that they do not develop in relation to any of the muco-cartilaginous prebranchial arches which in Ammocoetes would be represented by a "subaural" and a "perioral" arch.

According to DAMAS (1935), the posterior dorsal cartilage ("plaque prétrabéculaire") develops in the connective tissue entirely without any contact with the rostro-dorsal plate. The anterior dorsal cartilage, the annular cartilage, the stylet cartilage and the posterior lateral cartilage ("cartilage du toit, annulaire, les épines, cartilage rhomboïde") originate, according to him, in the new-formed connective tissue ("proviennent du tissu conjonctif de néoformation").

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According to HOLMGREN and STENSIÖ (1936), the posterior and anterior dorsal cartilage and the posterior lateral cartilage develop in one continuous procartilaginous mass. The annular cartilage and the stylet cartilage are supposed to belong to another system, originating from muco-cartilage in the tentacular bases.

According to BALABAI (1935) and HOLMGREN and STENSIÖ (1936) all rostral cartilage elements develop in a continuous mesenchyma in which, primarily, no separate blastemas can be discerned. As stated in the description of stages, this is the case especially in the region of the trabecular commissure where, at certain stages, the blastemas cannot be distinguished from each other.

The posterior dorsal cartilage is, undoubtedly, formed from a blastema in the caudo-medial parts of the rostro-dorsal plate. When, in this instance, other opinions have been suggested, the explanation is probably that the initial developmental stages have been missing. It should be mentioned here that, as stated by SCHAFFER (1896), the histological structure of this cartilage clearly differs from that of other cartilage elements in this region. At early stages, there is also a fusion between the rostral parts of the subocular arch and the posterior dorsal cartilage.

As appears from the descriptions of stages great difficulties will attend any attempt to fix a boundary, in the rostral region of the cranium, between mesenchyma derived from muco-cartilage and mesenchyma formed in dissolved musculature. The blastema that gives rise to the originally binary primordium of the anterior dorsal cartilage is, to judge from its position, for the main part or, possibly, entirely produced from dissolved musculature. As regards the posterior lateral cartilage, HOLMGREN and STENSIÖ state that "bei der nicht

metamorphosierenden Larve scheint ein besonderer Schleimknorpel hier nicht vorhanden zu sein". Nevertheless, this element was supposed to develop from a presumed thin layer of muco-cartilage, close to the pharyngeal wall, and from the lower part of the rostro-dorsal plate. In this, as in other instances, the explanation of the contradictory literary data must simply be that the stages available for observation have been too few. Many metamorphic stages would, no doubt, be extremely difficult to interpret without access to closely consecutive stages.

As to the origin of the anterior lateral cartilage, early writers on the subject have made no observations. Only BUJOR (1890—92) refers to its existence, supposing that it is formed in the same way as the other rostral cartilages. As to TRETJAKOFF (1926 a, 1929 a), a connection exists between the anterior dorsal and the anterior lateral cartilage. BALABAI (1935) emphasizes that the anterior lateral cartilage is changed into cartilage later than the other rostral cartilages. DAMAS (1935) mentions the existence of a connection between the apical cartilage and the anterior lateral cartilage. Like the apical cartilage, the latter should have developed from the connective tissue in the medial tentacle. HOLMGREN and STENSIÖ (1936) consider that the anterior lateral cartilage arises from muco-cartilage in the lateral mouth plate.

It has been mentioned in the descriptions of stages that the anterior lateral cartilage develops from a blastema, deriving from the particularly thick membrane of connective tissue that separates the muco-cartilage in the lateral mouth plate from the epithelium in the cavity of the mouth. Between this blastema and the muco-cartilage, or the derivative from it, a nerve and a vessel run (cf. Stage 6). Further, in one case, cartilaginous elements have been observed in the muco-cartilage of the lateral mouth plates. Yet a completely normal primordium of an anterior lateral cartilage is formed medially to it. BALABAI is quite correct in stating that this primordium changes into cartilage late. In fact, as shown in the descriptions of stages, it is formed early, with a far larger extension than its final shape would suggest.

SCHNEIDER (1879, p. 57) writes as follows: "In der Längsleiste, welche sich in der Bauchlinie der Mundhöhle erhebt, liegt ein langer Vorknorpel (here=muco-cartilage) zu dem in dem Tentakel noch ein zweiter kommt. Er dürfte dem Zungenstiel und der Copula als Grundlage dienen." KAENSCHE (1890) offers a more detailed account. He states, inter alia, that the apical cartilage and the piston cartilage develop from muco-cartilage in the medial tentacle and the ventro-medial longitudinal bar, respectively, originally in one single piece. The differentiation into two pieces takes place later. KAENSCHE mentions, further, that the medio-ventral cartilage ("die Copula") originates from a muco-cartilage portion, ventrally to the medial tentacle and dorsally to the ventro-lateral plate, i.e., in the commissure between the lateral mouth plates. BUJOR (1890—92) expresses similar views. According to him, however, the

piston cartilage arises "dans le jeune tissu conjonctif", resulting from the breaking-down of the muscles ventrally to the medial tentacle.

TRETJAKOFF (1929 a), who absolutely denies any histogenetic connection between muco-cartilage and cartilage, seems, none the less to hesitate, when discussing the piston cartilage. He writes (p. 509) as follows: "Man könnte höchstens von der Verwandlung der oben von mir erwähnten sagittal gestellten gallertigen Platte in die Cartilago glossa (hinterer Stempelknorpel, Basihyale nach PARKER) sprechen." He adds, however, that, according to his own observations, the possibility of a direct transformation of muco-cartilage into cartilage need in no case be taken into account.

DAMAS (1935) is of the opinion that muco-cartilage does not exist in the medial tentacle in the Ammocoetes larva. His logical conclusion is that the apical cartilage has formed in the connective tissue of this tentacle. In his opinion, the piston cartilage originates in the muco-cartilage of the ventro-medial longitudinal bar. The medio-ventral cartilage develops—according to DAMAS—from the ventral commissure between the lateral mouth plates, i.e., also in this instance, from muco-cartilage. According to HOLMGREN and STENSIÖ (1936), not only the piston cartilage and the apical cartilage but also the so-called anterior apical cartilages are derived from muco-cartilage.

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There is hardly any doubt as to the origin of the piston cartilage. It is, obviously, formed exclusively from muco-cartilage in the ventro-medial longitudinal bar in the larva. The apical cartilage seems to form in the tissue in the medial tentacle of the larva. In this case probably, both muco-cartilage and fibrous connective tissue are involved. Anyhow, like the binary anterior apical cartilages which appear later, the lateral process, which forms the primordium of the anterior lateral cartilage, is entirely formed in fibrous connective tissue. The anterior apical cartilages have their origin in the collagenous connective tissue close to the mucous membrane, and should be regarded as supports to the corneous teeth of the tongue.

The medio-ventral cartilage develops, as stated in the descriptions of stages, in the ventral part of an extensive blastematic area. It includes also the primordia of the ventral part of the annular cartilage and of the stylet cartilage. In this region extensive changes of position take place, a fact which renders less probable the supposition that muco-cartilage should be the only source of the cartilage formed in this spot.

SCHNEIDER (1879) assumed that the velar skeleton in the fullgrown animal had its origin in the lateral velar skeleton in the larva. His views were shared by KAENSCHE (1890) and, at first, also by DAMAS (1935) who, however, in a later work (1944), suggests the medial velar skeleton as the origin of the velar skeleton. HOLMGREN and STENSIÖ (1936) state that the velar skeleton develops in the muco-cartilaginous velar skeleton in the larva, though without specifying which of the two velar skeletons they have in mind. However, there

is no doubt that the cartilaginous velar skeleton in the full-grown animal is derived from the medial velar skeleton of the larva.

The changes in the branchial region have long been well known. SCHNEIDER (1879) mentions that the pericardial cartilage is not formed ("präformiert") from muco-cartilage. NESTLER (1890) and BUJOR (1890—92) briefly sum up the differences between the branchial basket in an Ammocoetes and a fully developed Petromyzon. SCHAFFER (1896) traces the origin of the new-formed cartilage in the branchial basket back to the small muco-cartilaginous elements he has observed there.

The descriptions of stages in the present investigation indicate that the cartilaginous blastemas in the branchial basket are formed at an early stage of the metamorphosis, though afterwards developing in a strikingly slow manner. The presence of muco-cartilage is not, it would seem, necessary for the formation of cartilage in the branchial region. Certain skeletal processes arise in places where no muco-cartilage is present. Moreover, the epitrematic longitudinal bar is supplemented outside the muco-cartilaginous area.

The cartilaginous rings, observed by NESTLER (1890), round the exterior gill openings in Petromyzon Planeri, are formed at a late stage of the metamorphosis, in the connective tissue underneath the epithelium.

KAENSCHE (1890) mentions the existence of the cartilaginous nasal capsule in the larva and proceeds to describe its development during the metamorphosis in the following words (p. 223): "Von ihn aus geht die Bildung der vollkommen knorpeligen Nasenkapsel des Petromyzon in der Weise vor sich, dass er im Perichondrium nach vorn, hinten und seitlich auswächst." The "perichondrium" referred to is, as a matter of fact, the entire fibrous nasal capsule. The descriptions by BUJOR (1890—92) and DAMAS (1935) conform on the whole to that by KAENSCHE. Apart from this normal appositional growth, a special type of interstitial development of the cartilage in the nasal capsule has been observed. This has been dealt with more in detail above (p. 187).

Concerning the development of cartilage in the neural cranium KAENSCHE (1890, p. 232) makes the following remarks: "Die Platten des Perichondriums sind hier bei Ammocoetes nicht durch Schleimknorpel getrennt, sondern schliessen fest an einander. In ihrem Innern treten, zunächst gesondert von einander, kleine Zellkomplexe auf. Dieselben vergrössern sich sehr rasch durch Teilung und vereinigen sich schliesslich mit einander." BUJOR (1890—92), DAMAS (1935) and HOLMGREN and STENSIÖ (1936) have, broadly speaking, adopted the same views. HOLMGREN and STENSIÖ state, contrary to SCHAFFER (1896), that the perichondria of the original cartilaginous elements do not play any considerable part in the formation of cartilage. The lateral walls of the cranium and the rostral part of the cartilaginous lamella that closes the anterior part of the fenestra basicranialis are developed by means of appositional growth. Further, the notochord is surrounded by cartilage immediately

caudally to the tip. Finally, the auditory capsules, on a broad basis, attach to the parachordalia.

As to the origin of the perichardial cartilage, DAMAS (1935) should be referred to.

V. CONCLUDING REMARKS REGARDING THE CRANIUM OF PETROMYZON.

The anatomy of the larval skull is very different from that of the adult. From histological point of view also great differences are to be found, due chiefly to the absence of muco-cartilage in the adult. Some authors have attributed a certain significance to this fact. In their opinion, muco-cartilage represents a primitive type of tissue. This view has played a part in phylogenetic discussions (cf. chapter VII), where, however, the occurrence of cartilage has also been taken into consideration. For this reason the genetic as well as phylogenetic relations between muco-cartilage and cartilage have to be subjected to close study.

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An investigation of the metamorphic changes will provide material for the understanding of the homologies between larval and adult elements in the skull. This subject will be discussed in connection with the question of the existence of so-called prebranchial arches (SEWERTZOFF 1916—17). The question in which degree the particular features in the cranial structure in Petromyzon are to be regarded as primitive or not, will be dealt with later (cf. chapter VII).

1. THE RELATION BETWEEN MUCO-CARTILAGE AND CARTILAGE.

As previously stated, typical muco-cartilage forms late during ontogeny. The cartilage elements in the branchial region develop far earlier. They form in the same ectomesodermal cell layer as does the muco-cartilage. The basal cartilaginous elements of the skull also develop before the forming muco-cartilage has lost its character of embryonic mesenchyma.

According to DAMAS (1944), cells of a procartilaginous type appear in the medial velar skeleton and in the caudo-dorsal rim of the ventro-lateral plate, before muco-cartilage has developed in these places. An identical course of development is seen also in the commissure between the trabecles, on a level with the medial velar skeleton, as described in this work. To judge from the present material, the tissue will hardly attain a typical procartilaginous stage in these places, although a peculiar differentiation is evident in the cells to be found there. The cells in these regions lie more densely than elsewhere in the tissue forming muco-cartilage. Likewise, a development of intercellular sub-

stance is observed, though the cells do not obtain the vesicular shape characteristic of procartilage. A small cartilaginous process forms on the ventral surface of the trabecle, as previously shown. The commissure mentioned fuses with this process. The tissue in the caudo-dorsal rim of the ventro-lateral plate, immediately attaching to the ventral part of the first branchial arch, as described by DAMAS, has a similar appearance. Later the peculiar features of these tissue elements disappear, and they take part in the muco-cartilaginous complex.

SCHAFFER (1896) has observed a small cartilaginous nodule in the muco-cartilage in a 9 cm larva. This cartilaginous element was situated on the dorso-caudal rim of the ventro-lateral plate, i.e. in the exact position in which DAMAS discovered the forementioned formation of procartilage in the ventro-lateral plate. The local occurrence of this cartilage nodule may readily be assumed to be the direct result of the process described by DAMAS. In this region cartilage (the extra-hyal) will normally develop only during metamorphosis.

In the present investigation also some cases of cartilage formation outside the area of its normal occurrence have been noticed, inter alia in two specimens with cartilage structures within the muco-cartilage. These structures had the same position in both these cases, viz. in the ventral portion of the lateral mouth plate. In one instance there was a small cartilage nodule on one side, in the other there were three cartilaginous nodules on one side and four on the other. During metamorphosis cartilage does not form in these areas. Consequently, there can be no question here of an abnormally early development of cartilage. The fact that cartilage has formed in the same place in two different specimens has been interpreted here as an indication of a tendency towards formation of cartilage in a place where cartilage in earlier phylogenetic stages may have existed as normal components of the skull (see p. 255).

Ontogenetically muco-cartilage never develops as an intermediate stage in the formation of cartilage. The observations rather suggest the opposite, at least in certain places. At the base of the lateral mouth plate and in the caudo-lateral edge of the ventro-lateral plate, cartilage sometimes seems to develop where muco-cartilage is normally the only skeletal tissue. Moreover, muco-cartilage forms very slowly. These facts suggest that muco-cartilage is a secondarily developed tissue in comparison to cartilage.

Muco-cartilage has occasionally been supposed to be a form of tissue closely related to real cartilage (e.g., SCHAFFER 1896). To some extent these two kinds of tissue resemble each other, especially as to the properties of the matrix. The shape of the cells, however, is not a sound basis for a comparison of this kind, though branched cells may be found in cartilaginous or cartilaginoid connective tissue in a number of animals without any close relationship with Cyclostomes.

The forming muco-cartilage keeps for an exceedingly long time the character of an embryonic mesenchyma and, even after the gradual development of its

typical structures, the cells retain the chief features of shape and mutual contact that characterize the embryonic cells of mesenchyma. The embryonic mesenchyma is, in fact, among the relatively few tissues where the matrix stains metachromatically (HOLMGREN, H. 1940, cf. DEMPSEY and WISLOCKI 1946). The conspicuous similarity between muco-cartilage and embryonic mesenchyma seems to deserve some attention. The subject will be discussed later. Certain phenomena connected with the forming of cartilage will be dealt with first.

In the course of metamorphosis cartilage will form in mesenchyma deriving from muco-cartilage, as well as from other kinds of connective tissue. In certain places blastemas are formed, apparently histologically identical with ordinary cartilage-forming blastemas. These blastemas do not however change into cartilage but disappear. This is the case in the dorso-caudal part of the extra-hyal, in the ventral part of the hypothetical extramandibular (see p. 251) and in the region dorsally to the primordium of the posterior dorsal cartilage (the dorso-lateral blastema). On account of their position and their relation to other organs, and histological conditions (see chapter IV), these structures may be interpreted as blastemas which, for some reason or other, fail to develop. The actual blastemas forming cartilage often possess an extent that in no way corresponds to the fairly inconsiderable volume of the later forming cartilaginous elements. This refers, it would seem, in particular to the rostral cartilage elements. They form in certain blastematic portions which gradually develop in the original, comparatively polynuclear and very extensive mesenchymatic area. The other portions of this area gradually break down, and are replaced by blood sinuses. During certain phases of metamorphosis some of these cartilage elements are united by fairly well developed cartilaginous parts (e.g., the anterior dorsal cartilage with the posterior lateral cartilage, and the stylet cartilage with the annular cartilage) which, however, afterwards become markedly reduced or change into connective tissue. The forming of the anterior lateral cartilage—the blastema of which is originally extremely polynuclear and large-sized and is in contact with the primordium of the apical cartilage—takes place late. The anterior lateral cartilage is small, and the larger part of the blastema vanishes. A series of accessory cartilaginous processes develop on the branchial arches. In this case, the process is, however, different. Here cartilage develops fairly early close to the branchial arches. The cartilage is relatively well developed in their vicinity, while, distally, a gradual change into less and less highly differentiated cartilage is observed. However, these early processes soon stop. The tissue remains, partly, at an undeveloped stage. The same process is observed, for instance, in the cartilage filling the space between the ventral longitudinal bars.

In certain cases no cartilage, but so-called vesicular supporting tissue, develops from the blastemas formed in the course of metamorphosis ("chondroides

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Stützgewebe", SCHAFFER 1930). In the opinion of SCHAFFER (1897, 1903), this tissue is closely related to cartilage. In certain places a gradual change from one to the other of these two types of tissue can be observed, e.g., laterally to the middle part of the piston cartilage, where cartilage exists in the centre of a formation of vesicular supporting tissue (fig. 60). This tissue has a considerable extent in the vicinity of some of the rostrally situated cartilage elements (fig. 57).

Abnormal development of cartilage has been observed also outside the area of muco-cartilage. This was the case in one specimen, on one side of the parachordal cartilage, and in another between the first branchial arch and the extra-hyal. In a third specimen it was observed in the second branchial arch and, in a fourth, in the subchordal longitudinal bar. SCHAFFER (1896) describes a case in which the subchordal longitudinal bars meet in the median line, ventrally to the notochord. SEWERTZOFF (1916—17) observed certain cartilaginous processes on the branchial arches in the larva.

Assuming that the ancestors of Petromyzon actually possessed a well developed endo-skeleton—a hypothesis supported, it seems, by sound evidence (cf. chapter VII)—the forementioned facts might be explained as signs of an earlier, more extensive distribution of cartilage. This would, at the same time, suggest that a reduction in the development of cartilage has taken place during the evolution of Petromyzon and we are therefore justified in asking whether any definite indications of such a reduction are actually to be found in these animals.

At certain stages in the metamorphosis, the new-formed cartilage regularly breaks down in the ventral part of the extra-hyal. The points of attack are always situated symmetrically in the ventral part of the two extra-hyal arches (fig. 54). Cartilage cells and intercellular substance break down and disappear completely. The lacunae thus formed enter into open communication with such lacunae as arise outside the cartilage, through the breaking-down of remains of the muco-cartilage in the ventro-lateral plate, lying adjacent. It might be suggested that the part of cartilage in Petromyzon next in turn to disappear—owing to the continuous reduction of the cartilaginous cranium which seems to take place during evolution—would be that very part of the extra-hyal. At any rate, it seems possible that the forementioned process of destruction will fit in with such a hypothesis.

Another type of breaking-down of cartilage is to be noted in the nasal capsule and the pedicle process (p. 187). However, in this case, it seems to be a matter only of a special form of growth, as here nothing but the intercellular substance is dissolved. The cells remain and take part in new formation of cartilage in the parts concerned. In the extra-hyal some kind of healing process must also follow the breaking-down, as in old specimens no trace, in the form of excavations or such-like, can be observed in the cartilage. Nevertheless, an

essential difference between these processes remains, in so far as the cells in the extra-hyal are destroyed, contrary to what happens in the other cases.

It has been suggested above that, on one hand, muco-cartilage may be a tissue formed secondarily to cartilage and, on the other, that cartilage, to judge from various signs, may have had a more extensive distribution at earlier stages of evolution than at present. Naturally, the question follows: can, then, any conceivable explanation be offered regarding the appearance of muco-cartilage during evolution?

In the larva of Petromyzon the eyes remain at a relatively undeveloped stage. Only during metamorphosis do they enter upon a phase of definitive development. During the metamorphosis the so-called subocular musculature also appears, though the primordium has formed at a comparatively early embryonic stage. Its development stops and the embryonic character of the primordium remains till the end of the larval period (DAMAS 1935). The slow development of muco-cartilage may, possibly, be interpreted as an indication that muco-cartilage also represents a primordium that has been delayed in developing. Only when the larva has grown in size, but not before, do specific differentiations of the cells become visible. Indeed, the similarities with embryonic mesenchyma remain until the beginning of the metamorphosis. At this stage the muco-cartilage is either changed into cartilage or possibly into some other form of connective tissue, or it is destroyed.

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This explanation is, of course, a mere hypothesis. Definite proofs of the phylogenetic origin of muco-cartilage are hardly possible to obtain from facts that exclusively concern the ontogeny. Since, however, muco-cartilage is known only in the larva of Petromyzon, it seems reasonable to base an opinion on this subject on available facts regarding origin, development and transformation of this tissue in this animal.

2. THE CRANIAL MORPHOLOGY OF PETROMYZON.

SEWERTZOFF (1916—17) made an attempt to trace in the larva such elements as would correspond to the cartilaginous structures in the full-grown Petromyzon. His knowledge of the course of metamorphosis, which is the natural basis of such a study, was, however, deficient. In connection with this problem he also entered into the question of the branciomere construction of the visceral cranium of Petromyzon.

Moreover, from a comparison between the functioning branchial arches and the cartilaginous elements, situated rostrally to, and, in his opinion, homodynamic with certain parts of these branchial arches, SEWERTZOFF tried to distinguish parts that, one by one, would be homodynamic with parts of the branchial arches. As stated before, there are in the branchial region of the full-grown animal, as well as of the larva, four more or less distinctly devel-

oped longitudinal bars, viz., the subchordal, the epitrematic, the hypotrematic and the ventral longitudinal bar. SEWERTZOFF thus endeavoured to trace the homodynamic equivalents in the prebranchial cartilage elements of these longitudinal bars and the parts of the branchial arches situated between them. His conclusions were set forth in two schematic figures (SEWERTZOFF 1916—17, figs. 6 and 7).

The "hyoid arch", i.e. the extra-hyal is, caudally, connected with the branchial basket, normally by means of two cartilaginous bars. The ventral bar obviously forms a direct continuation rostrad of the ventral longitudinal bar, and is interpreted in this way by SEWERTZOFF. The dorsally situated bar is supposed to constitute a rostral prolongation of the hypotrematic longitudinal bar. This interpretation is explained by the fact that this connecting link from the extra-hyal fuses with the ventral, horizontal part of the cartilaginous loop that runs round the first gill slit. This loop seems, in its turn, to be a direct extension rostrad of the hypotrematic longitudinal bar. The corresponding part, dorsally to the gill slit, is supposed to be a part of an epitrematic longitudinal bar which, however, never comes into contact with the extra-hyal. Instead, the rostral part turns ventrad, and fuses with the hypotrematic longitudinal bar.

However, in the present investigation a small pad of procartilage has been observed during the metamorphosis (e.g., Stages 6 and 12), rostro-dorsally on the epitrematic part. This pad might be regarded as a rest of the missing part of this longitudinal bar. Further, at Stage 14, an interesting aberrant formation of the cartilaginous parts between the extra-hyal and the first branchial arch has been described. Here an entire epitrematic longitudinal bar has, apparently, developed while a hypotrematic one is, simultaneously, situated ventrally.

The attention has already been drawn to the existence of small cartilaginous processes directed towards each other from the epitrematic and the hypotrematic longitudinal bars in the branchial basket, immediately rostrally to the gill slits. It seems probable that the rostral part of the complete loop round the first gill slit is homodynamic with these processes.

Dorsally, the extra-hyal below the auditory capsule terminates in a horizontal cartilaginous rod, ending caudally without touching any other cartilaginous element, but rostrally fusing with the processus styliformis.

According to SEWERTZOFF, the extra-hyal in the larva is represented by the caudo-dorsal rim of the ventro-lateral plate. The part of the ventral longitudinal bar that belongs to the extra-hyal is then incorporated in the muco-cartilage in the caudo-lateral portion of the ventro-lateral plate. On the other hand, neither the hypo- nor the epitrematic longitudinal bar can be distinguished between the extra-hyal and the loop round the first gill slit in the larva. Dorsally, according to SEWERTZOFF, the caudal part of the subotic muco-cartilage portion which is fused with the dorsal piece of the first branchial arch, constitutes a prolongation rostrad of the subchordal longitudinal bar. The

caudally directed process in the dorsal part of the extra-hyal of the adult is in his opinion a remainder of the subchordal longitudinal bar.

The homologization of the caudo-lateral parts of the ventro-lateral plate with the extra-hyal, and the interpretation of the cartilaginous process caudad from the extra-hyal as a subchordal longitudinal bar, both meet with certain objections. The nervus hyoideus VII runs caudally to the caudal edge of the ventro-lateral plate and rostrally to the extra-hyal. This is, in fact, evident from SEWERTZOFF's own pictures. As previously shown (p. 235), the extra-hyal is, in the course of the metamorphosis, partly formed outside the area of muco-cartilage in the ventro-lateral plate, caudally to the mentioned nerve. This nerve runs between the two blastemas of the extra-hyal and the processus styliformis, otherwise not easily distinguishable. The middle part of the extra-hyal does not, therefore, seem to be represented in the muco-cartilage.

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The caudal part of the subotic muco-cartilaginous portion is, according to SEWERTZOFF, situated medially to the nervus glossopharyngeus. His statement, however, does not conform to actual facts, since this nerve, like the nervus hyoideus VII, runs medially to this muco-cartilage. For this reason the subotical muco-cartilage portion cannot, it would seem, be interpreted as a rostral extension of the subchordal longitudinal bar. This bar always lies medially to the nerves. Nor does this interpretation seem to be applicable to the caudally directed process in the dorsal part of the extra-hyal, since, according to SEWERTZOFF, it develops, during metamorphosis, from the mentioned muco-cartilaginous formation. With regard to the interpretation of the dorsal part of the extra-hyal, HOLMGREN (1946) suggests views similar to SEWERTZOFF's.

As shown above, the dorsal, caudally directed cartilaginous process of the extra-hyal could hardly be explained as a part of the subchordal longitudinal bar. Nor can it be interpreted as an epitrematic one, since, as mentioned before, parts of such a bar are, probably, present elsewhere. In SEWERTZOFF's paper there is no indication of any alternative interpretation.

In reconstructions of the metamorphosed cranium of Petromyzon, represented by SEWERTZOFF and other authors (e.g. PARKER 1883, HOLMGREN and STENSIÖ 1936), a number of rostrally and caudally directed processes are seen on the branchial arches. In the present investigation these cartilaginous processes have already been interpreted as possible manifestations of a tendency to cartilage-formation which, at earlier phylogenetic stages, may have been more extensive. They do not form continuous longitudinal bars, though an indication of such bars may, possibly, be found in the larger processes, projecting towards each other from the different branchial arches. One set of such processes is present dorsally to the epitrematic longitudinal bar, another ventrally to the hypotrematic one. These processes may be the remains of a latero-dorsal and a latero-ventral longitudinal bar. Whether or not the other cartilaginous protuberances on the branchial arches, which are without any

opposite partners on neighbouring branchial arches, are also to be regarded as remains of such longitudinal bars, or whether they have any other significance, cannot be decided at the present state of our knowledge.

A connection between a rostrally and a caudally directed process is clearly visible only in one place. In the larva the subotical muco-cartilage portion occupies such a position as to unite the parts where, during metamorphosis, the caudally directed cartilaginous process dorsally on the extra-hyal and the rostrally directed process on the first branchial arch develop. During the metamorphosis a blastema forms at this position between the first branchial arch and the extra-hyal. From the rostral and caudal parts of this blastema the two cartilaginous processes originate, while the intermediate blastema portion breaks down without changing into cartilage. This course of development appears to support the idea that a connection may have existed between the cartilaginous processes, at least in this position. This would mean that, consequently, a latero-dorsal longitudinal bar might have previously existed here.

The rostral part of the subotical muco-cartilage portion SEWERTZOFF interprets as an epitrematic longitudinal bar. HOLMGREN (1946), on the other hand, regards it as a subchordal one ("basal parts of external arches"). HOLMGREN's opinion does not seem based in fact, as the nerves run medially to this structure. It appears impossible, however, to determine whether this structure constitutes a rostral extension of a latero-dorsal longitudinal bar (cf. above) or, as SEWERTZOFF assumes, of an epitrematic longitudinal bar. The similarity in position between these two structures is so marked that it is difficult to distinguish between them, when they are not simultaneously present. From the metamorphic process it is evident that, in the full-grown animal, this part of muco-cartilage corresponds to the cartilaginous portion that connects the extra-hyal and the dorsal part of the styliform cartilage.

While SEWERTZOFF's idea that the different structural units of the branchial arches can be traced in prebranchial elements seems easily applicable to the extra-hyal, it is, as mentioned by HOLMGREN (1946), far less relevant to other prebranchial elements.

SEWERTZOFF considers that, apart from the extra-hyal, four additional prebranchial arches can be identified in the full-grown Petromyzon, while in the larva only two of these are developed. TRETJAKOFF (1929 a) on the whole agrees, though rejecting SEWERTZOFF's notion of homologous equivalents in the muco-cartilage of any branchial arches. STENSIÖ (1927) expresses the opinion that not more than three prebranchial arches are present in Petromyzon. He mentions, inter alia, that SEWERTZOFF has been unable to detect more than this number in the larva, and that, according to KOLZOFF, not more than three somites appear, rostrally to the auditory capsule, in the course of the embryonic development. Further, the related Osteostraci posses obviously only one

premandibular branchial arch. DAMAS (1944), HOLMGREN and STENSIÖ (1936) and HOLMGREN (1942, 1946) likewise base their reasoning on the view that in Petromyzon there is only three prebranchial arches to be traced. As early as in 1900, GASKELL specified this number of arch elements in Ammocoetes.

SEWERTZOFF interprets the processus styliformis as a prebranchial arch, "arcus praebranchialis 2". In his opinion, the corresponding part in the larva is represented by the pedicle process and by a muco-cartilaginous ridge along the base of the velum. Here, SEWERTZOFF possibly had in mind the lateral velar skeleton. According to SEWERTZOFF, the pedicle process is formed between the trigeminal ganglion and the facial ganglion. Because of the histological similarity between the cartilage in this structure and that in the branchial elements, on one hand, and, the dissimilarity, in the same respect, between the cartilage in the pedicle process and that in the "parachordalia", on the other, he arrives at the conclusion that the pedicle process constitutes the dorsal part of a visceral arch. On account of its relations to the nerves, he concludes that the mandibular arch is in question here. HOLMGREN (1946) has suggested that the pedicle might be "a basitrabecular process". Therefore, it does not belong to the visceral cranium. This subject will be dealt with later (p. 259).

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During metamorphosis, the processus styliformis does, however, not form from material from the lateral velar skeleton. At any rate, it does so only to an exceedingly small extent (cf. p. 237). In fact, the styliform cartilage seems to develop from various sources. If it corresponds to a prebranchial arch in the full-grown animal, this arch is not, apart from the portion that constitutes the pedicle process, present in the larva.

In the opinion of SEWERTZOFF, the cornual cartilage would form a rostral part of the hypotrematic longitudinal bar. However, since the cornual plate is penetrated by the nervus mandibularis V, the cartilage in it lies, at least partly, medially to the nerve belonging to the arch, thus differing from a normal branchial arch of Petromyzon. On this point HOLMGREN (1942, 1946) does not agree with SEWERTZOFF. HOLMGREN suggests that the cornual cartilage does not correspond to any part of a branchial arch in Petromyzon, an opinion shared by the present author. This subject will, however, be dealt with later (Chapter VI). The way in which the cornual plate is formed during the metamorphosis, does not support SEWERTZOFF's opinion.

In connection with the description of the metamorphic process, mention was made of the fact that, at the early stages of the metamorphosis, a blastema seems to connect the portion of the primordium of the processus styliformis that has its origin in the muco-cartilage of the ventro-lateral plate with the primordium of the ventral longitudinal bar in the extra-hyal. The blastemas of the extra-hyal and the processus styliformis are, on the whole, formed in close proximity to each other. At first, they can be distinguished only because of the fact that the nervus hyoideus VII runs between them. This inconsiderable

distance between the two primordia, which, none the less, are supposed to represent two different arches, is, probably, due to the reduction of the intermediate branchial sac during ontogenesis. This reduction has been studied in detail by DAMAS (1944, fig. 223). The small distance between these formations can, therefore, not be referred to as proving that they should belong to the same arch, as believed by BALABAI (1935). The existence of the ventral blastematic connection between the primordium of the processus styliformis and the ventral longitudinal bar in the branchial basket may seem to support the suggestion that the processus styliformis should include at least a part element homodynamic with a branchial arch. The processus styliformis is, in fact, generally regarded as a branchial element belonging to the mandibular segment. HOLMGREN (1946) calls it "extra-mandibular".

From the dorsal part of the processus styliformis a cartilaginous bar, the so-called subocular arch, projects rostrad. SEWERTZOFF regards it as an epitrematic longitudinal bar. HOLMGREN considers the subocular arch to be a continuation of the subchordal bar, an opinion that seems to be contradicted by the fact that in this case, also, the nerves run medially to it.

According to SEWERTZOFF, the third prebranchial arch in the larva is identical with the lateral mouth plate, while, in the full-grown animal, it is supposed to correspond with the cartilaginous bar that connects the horizontal part of the subocular arch with the trabecular commissure. This homologization is apparently deducted from SEWERTZOFF's supposition that, during the metamorphosis, the lateral mouth plate has been transformed into this vertical part of the subocular arch. HOLMGREN and STENSIÖ (1936) point out the error of this assumption. In their opinion, the anterior lateral cartilage has its origin in this portion of muco-cartilage. As seen in the present investigation from the description of the metamorphic process, this latter statement is incorrect. The anterior lateral cartilage derives from a blastema formed medially to the lateral mouth plate in the strongly developed connective tissue below the epithelium in this particular region. This cartilaginous formation is regarded by HOLMGREN (1942, 1946) as a premandibular element, though, for certain reasons, it is not homodynamic with other branchial arches in Petromyzon. This matter will be discussed later (chapter VI). SEWERTZOFF terms the anterior lateral cartilage the "arcus praebranchialis 5".

The connection between the rostral part of the subocular arch and the trabecular commissure (the vertical part of the subocular arch), and the posterior lateral cartilage, i.e. SEWERTZOFF's "arcus praebranchialis 3 and 4", are by HOLMGREN (1946) considered to belong to "an external system of cartilages".

DAMAS (1944) rejects the idea that elements, or parts of elements, homodynamic with branchial arches, exist rostrally to the extra-hyal. He points out that, apart from the pedicle process, the ventro-rostral skeleton in the larva

consists of muco-cartilage only ("membranes élastiques") and that this is derived from an ectomesodermal layer that is continuous from the beginning. When this tissue has been partly pushed aside by other organs, especially muscles, the muco-cartilaginous skeleton, characteristic of the full-grown larva, begins to form. DAMAS refutes SEWERTZOFF's idea of the development of primarily separate, vertical muco-cartilaginous arches, homodynamic with branchial arches. According to DAMAS, there are only two segments to be found in the large rostral region of the animal, the mandibular and the premandibular segments. He doubts the possibility of identifying the limit between the ectomesodermal components belonging to these two segments. Nevertheless, he states that only the rostro-dorsal plate, "la plaque élastique prénasale", belongs to the premandibular region, while the muco-cartilage complex, which includes the lateral mouth plates (except the particular part from which the extra-hyal derives), pertains to the mandibular area.

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Thus, DAMAS, who particularly stresses that he is referring to regions and not to arches, makes the limit between the two regions, as far as the ectomesodermal components are concerned, coincide with the rostral border line of the musculature derived from the mandibular segment. It is, however, far from certain that the strong development of this musculature in Ammocoetes is primitive. It is, therefore, open to question wether this musculature forms a satisfactory basis for the drawing of a demarcation line. On account of neurological conditions, TRETJAKOFF (1927 a, 1929 a) arrived at an entirely different conclusion with regard to the segmental division of the cranium of Petromyzon. In this respect, his views were similar to SEWERTZOFF's. HOLMGREN (1942, p. 122) states that "all those muscles which are innervated by the suborbital branches of the trigeminal (V 2) of Petromyzon belong to the prenasal skeleton". It seems probable to the present author that the boundary between the ectomesodermal components in the mandibular and premandibular segments lies caudally to the lateral mouth plates, approximately corresponding to the border line between the mandibular and premandibular segments, at relatively early embryonic stages. No definite reasons can support this statement, neither can any decisive argument be found in favour of the views of DAMAS. The lateral mouth plates, dorsally fusing with the rostro-dorsal plate, may, thus, form part of the premandibular region.

According to the results of experimental embryology, cartilage can only develop in the branchial arches of Amphibia under certain conditions, one of which is the presence of entoderm in the branchial region. The entoderm seems to induce the process of cartilage formation (RAVEN 1941—42, HÖRSTADIUS und SELLMAN 1946). It may, of course, be a matter of dispute whether or not results from this material can be concidered generally applicable. As to Gnathostomes this seems to be the opinion generally accepted. An attempt to widen the base of the discussion to include also Cyclostomes can obtain

but little support from available facts. As regards Myxine, NEUMAYER (1937) accepts the possibility of the formation of the branchial arches being induced by entoderm. Furthermore, DAMAS (1944) points out the exceedingly good conformity between his own results and those arrived at by experiments, principally those published by STONE (1929). There are, however, as will be dealt with later (see Chapter VI), considerable differences in the relative position between the branchial arches of, respectively, Gnathostomes and Cyclostomes, a fact which unfavourably affects the value of the following discussion. Still, in both groups there are branchiomere cartilaginous elements of an ectomesodermal origin. Considering that experimental investigations in the case of Petromyzon will meet with considerable difficulties (DAMAS 1944), it will, unfortunately, not be possible to form an obviously correct opinion on this subject. In that case there seems to be justification to pay regard—with all due reservations—to the data produced by means of experimental embryology.

At once it may be stated that the entire rostral complex of muco-cartilage and buccal and visceral cartilage in the grown-up larva, as well as in the adult animal, borders to the stomodaeum. Since, in this formation, the epithelium is of an ectodermal origin, the possibility of ascribing an entodermal induction to these elements is evidently, at late stages, excluded.

In young embryos of Petromyzon the coming stomodeal invagination is indicated merely as a ventral thickening of the ectodermal epithelium. When about 30 segments have developed, the invagination process sets in. At these early stages entoderm is situated dorsally to this part, i.e. rostrally to the ectoentodermal border line in the grown-up larva. In the literature an almost complete agreement seems to prevail regarding the fact that this limit adjoins to the caudal side of the velum. The velum is, in fact, simply formed by the part in which ectoderm and entoderm meet rostrally. In the course of the development, certain changes in position of the rostral part of the entoderm take place, but they will only result in moving the entoderm laterad to the caudal side of the velum and of its final attachment, laterally to the velar base (DAMAS 1944).

At certain stages, when the ectodermal stomodeal primordium has invaginated dorsad and caudad, an entodermal cell streak will, as stated by CLAYDON (1938), be found immediately ventrally to the notochord. Rostrad, this entodermal streak gets more and more diffuse, and changes gradually into the scattered cells that fill the space between the caudal end of the hypophysis and the tip of the notochord. It seems probable that entodermal cells play a part in the formation of the hypophysis, as in the case of sturgeons (HOLMGREN 1931) and of Lepidosteus and sharks (LINDAHL 1944). This question will not, however, be discussed here. Yet, it is worth noting, in this connection, that entoderm exists rostrally to the place which is generally looked upon as the

boundary between ecto- and entoderm. Thus, it is possible that an induction from the entoderm may take place in the rostral region at early embryonic stages. Even at later stages such an induction seems possible from entodermal cells that are left rostrally to the border line indicated by the velum.

During metamorphosis no cartilaginous elements are formed in the lateral mouth plates. Even had the opposite been the case, it would have been open to question whether such a cartilage formation could have been induced by the entoderm, as cartilage does not form until years later during metamorphosis. With regard to the points of view maintained above, it seems doubtful if a muco-cartilaginous formation, such as the lateral mouth plate, could be regarded as homodynamic with a cartilaginous branchial arch. In this connection the occurrence of the previously mentioned (p. 156 and 244) aberrant cartilage nodules, in the larva of Petromyzon, may, perhaps, be considered as possessing a certain significance. The extrahyal is, at early stages, represented by a cell streak of a specific shape. As stated, SCHAFFER (1896) has, also, described a cartilaginous nodule in the same position as part of this cell streak in a full-grown larva.

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That cartilage has developed at the base of the lateral mouth plates in two different specimens seems to be of importance. Had this observation been made only in a single specimen, no conclusions could justly have been based on it. The probability of a mere chance occurrence of this cartilaginous formation seems to be considerably reduced by the fact that it has been discovered in exactly the same position in two specimens. The conclusion closest at hand would, it seems, rather be that a special tendency towards formation of cartilage is present in the muco-cartilage in this particular place. These cartilaginous nodules can be interpreted either as a remainder of a cartilaginous formation from earlier phylogenetic phases or as a manifestation of cartilage formation to come during evolution. The latter alternative appears to be less probable, partly because the structure of fossil Agnatha suggests a better developed endoskeleton in the ancestors of Cyclostomes, partly because of previous statements in part I of this chapter concerning the relation between cartilage and muco-cartilage. The particular area of muco-cartilage, where the forementioned cartilaginous nodules are situated, breaks down later in metamorphosis than do the adjacent regions of muco-cartilage.

Thus, if the lateral mouth plates can, at least partly, be regarded as homologous with previously existing cartilaginous elements, they could also be supposed to be homodynamic with branchial arches. The position of the lateral mouth plates makes it possible to consider them as premandibular arches. Since certain parts of the suborbital nerve (V) run on their inner side, they may represent an extra-premandibular.

There seems to be no reason to expect the existence of more than three prebranchial arches. In view of this fact the skeletal elements of the skull,

not dealt with in this chapter, must be of another nature. The development of these various cranial elements seems hardly to belong to any primitive state. Hovewer, this subject will be discussed later (Chapter VII).

VI. COMPARISONS BETWEEN PETROMYZON, MYXINE AND GNATHOSTOMATA.

1. TRABECLES AND PARACHORDALS.

The first investigators of this subject did not hesitate to homologize the anterior part of the skeleton in the cranial base of Petromyzon with the trabecles of Gnathostomes (HUXLEY 1875—76, CALBERLA 1877, PARKER 1883, KOLZOFF 1901, GAUPP 1906, and others). However, as early as in 1897, SEWERTZOFF drew attention to the fact that the trabecles were, in the literal sense of the word, formed parachordally. Partly on account of this fact, partly because the trabecular primordia in Petromyzon were supposed to be of somitic origin (KOLZOFF 1901), SEWERTZOFF, later, arrived at the conclusion that the entire skeleton of the cranial base of Petromyzon should be homologous with parachordal elements in Gnathostomes. According to SEWERTZOFF, the trabecles of Gnathostomes should be visceral elements. This opinion has, in fact, prevailed for a long time (cf. DE BEER 1937).

SEWERTZOFF's theory induced him to look for elements in Petromyzon that might be homologous with the trabecles of Gnathostomes. After an analysis, chiefly of the relations between several skeletal primordia in the cranium and the hypophysis of these two groups, he came to the conclusion that the trabecles were represented in the posterior dorsal cartilage in the full-grown Petromyzon and the rostro-dorsal plate in the larva.

To some extent, DE BEER (1931 a, 1937) adopts SEWERTZOFF's views, as he states that "the brain-case of Petromyzon is wholly chordal in composition". His statement is based on the theory that the trabecles, both in Cyclostomes and Gnathostomes, are "a visceral structure", belonging to the premandibular segment. While these formations in Gnathostomes fuse with the parachordalia and—according to DE BEER, secondarily—as trabecles take part in the formation of the cranial base, they are in Petromyzon supposed to be in their primary position as premandibular arch elements. Originally, DE BEER (1931 a) was of the opinion that these elements in the larva were represented by the lateral mouth plates. Since, however, muco-cartilage, according to his later views (1937), could not be supposed to constitute an arch element in the proper sense, he has suggested that the arch element, homologous with the trabecle in Gnathostomes, is the vertical part of the subocular arch in the metamorphosed Petromyzon. On the other hand, DAMAS has recently expressed the view that

the trabecles, which he regards as entirely ectomesodermal in Petromyzon, would be considered to be strictly homologous only with the rostral part of the gnathostomian trabecles which has the same origin.

Experimental investigations, principally on Amphibia, have shown that the caudal parts of the trabecles in these animals are not ectomesodermal (STONE 1929, RAVEN 1932, 1941—42, HÖRSTADIUS and SELLMAN 1946, among others). Further HOLMGREN (1940, 1943 a) has analysed the formation of the trabecles in various groups of gnathostomian fishes, and arrived at an identical result, viz., that their trabecles and polar cartilages are formed in the sclerotomes of the premandibular and mandibular segments, respectively. In their original primordia they, thus, appear to be somitic. However, during a later period of development ectomesodermal cell elements will be added rostrally and form the rostral part of the trabecles and the trabecular commissure. The conformance between, on one hand, these results, which rest on a comprehensive material, and those from the experimental investigations, on the other, is strikingly good.

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HOLMGREN (1946) rejects SEWERTZOFF's ideas. If the trabecles are ectomesodermal, they cannot be of parachordal nature. On the other hand, if they are mesodermal, i.e. somitic, they behave as normal trabecles in lower Vertebrates.

HOLMGREN's investigations appear to have thrown new light on the homologies between the trabecles in Petromyzon and Gnathostomes. The very reasons on which SEWERTZOFF based his conclusions regarding the "cornua parachordalia" are applied as evidence for diametrically opposite views. In addition, the trabecles in certain Gnathostomes are formed laterally to the notochordal tip (PEHRSON 1922).

ALLIS (1923—24 a, b) has suggested that trabecles and polar cartilages are to be regarded as the pharyngeal elements of the premandibular and mandibular arch respectively. Should the mentioned elements primarily be of a somitic origin, such an interpretation will lead no further than SEWERTZOFF's theory. For the same reason, DE BEER's interpretations appear as improbable.

DAMAS (1944) has recently suggested that the trabecles of Petromyzon are entirely ectomesodermal. As mentioned in the preceding pages, this statement cannot be accepted by the present author. The parabuccal cell band cannot, at any rate, be considered as a trabecular primordium in its primary position. The results of the present investigation agree chiefly with KOLZOFF's (1901).

In Petromyzon the caudal parts of the trabecles are, probably, of somitic origin and the material seems to derive from the sclerotomes in the first and second segments. In this animal, there is no division into two primordia, viz., polar cartilage and trabecles in a limited sense. Later, the trabecular commissure changes into cartilage, to some extent independently of the trabecles. This is,

possibly, due to the fact that the commissure is of a different, viz., ectomesodermal, origin. With regard to their origin, the trabecles in Petromyzon and Gnathostomes seem to agree in every detail. Earlier, the uniformity in the relations between the hypophysis and the trabecles, as well as between the trabecles and the notochord in Gnathostomes and Petromyzon, has repeatedly been pointed out (ALLIS 1922—23 b, DAMAS 1944).

The parabuccal cell band, i.e. DAMAS' trabecular primordium, lies ventrally to the arteria mandibularis which transiently appears, in the course of the ontogeny. This condition apparently agrees with the position of the trabecle in sharks, as regards this artery. In sharks, the arteria mandibularis runs dorsally to the trabecle, a fact which DE BEER (1924) has tried to explain. However, his hypothesis seems unnecessary, in view of the fact that the artery in question, as demonstrated by HOLMGREN (1943 a), is primarily formed ventrally to the polar cartilage and, then, moves dorsad between that element and the caudal part of the trabecular primordium, before these structures fuse. The correlation between the mandibular artery and the trabecle in sharks, thus, seems to be a secondary phenomenon.

Available embryological facts regarding Myxine and Bdellostoma are not sufficient to allow any definite conclusions as to the formation of the trabecles. Certain facts have been recorded by NEUMAYER (1938), who seems to have unreservedly accepted SEWERTZOFF'S views concerning the morphology of the cranial base in Cyclostoma. Taking into account NEUMAYER'S work, HOLMGREN, in connection with a description of an embryo of Myxine (1946), made an interesting comparison between Myxinoids and Gnathostomes.

In his Myxine embryo, HOLMGREN observed a blastematic connection between the trabecular primordia, rostrally to the so-called hypophysial commissure, which he interprets as a trabecular commissure, homologous with that of Gnathostomes. The hypophysial commissure in Myxine, i.e. NEUMAYER'S "hintere Gaumenplatte nebst Verbindungsknorpel" is by HOLMGREN homologized with the cartilaginous portions that, in Selachii, form the precarotid and postpituitary commissures. During their development, these elements in the basicranial fenestra are situated between the polar cartilages (HOLMGREN 1940). ALLIS (1903, 1923—24 b) has earlier made attempts to homologize the hypophysial commissure in Myxine with "the preclinoid wall of the Gnathostomes", but pointed out that the relative positions are, in this case, not entirely identical. Should the hypophysial commissure in Myxine be homologous with the mentioned cartilaginous elements in Selachii, then, HOLMGREN concludes, the parts of the trabecles related to these formations should also be homologous. This implies that "the posterior part of the trabecles with the commissure in Myxine belongs to the polar cartilage". "Then", he writes, "the trabecle sensu strictiori must be the anterior part of the trabecular system in front of the hypophysial commissure." He adds that "this question can, however, not be

definitely answered before the early development of the trabecles has been investigated in Bdellostoma or Myxine" (HOLMGREN 1946, p. 19).

In an earlier publication by the present author (JOHNELS 1944) it has been shown that a commissure—in the adult larva connecting the dorsal parts of the medial velar skeleton in the shape of a muco-cartilaginous bar—develops on a level with the mandibular segment. This commissure fuses with the parts of the trabecles, which develop in the mandibular segment and should, thus, be homologous with the polar cartilages of Gnathostomes. DAMAS (1944) has described the intimate connection between the medial velar skeletons and the trabecles but fails to observe the existence of the forementioned commissure. During certain stages of the larval development cartilage forms on the ventral surface of the trabecle, where the commissure is attached. In this way a small cartilaginous tip is formed, protruding towards the commissure and the medial velar skeleton. Both these elements consist of a dense blastema. From them a blastematic band runs caudo-laterad, along the surface of the trabecle, and fuses with the pedicle process.

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The commissure exists only in the larva and consists of muco-cartilage. During metamorphosis it breaks down. However, before this happens the naso-hypophysial tube grows caudad dorsally to it. In the larva, the carotid arteries, having just branched from the aorta dorsalis, pass rostrad, between the commissure and the notochord, into the cranial cavity.

It is possible to homologize this commissure in Petromyzon with the hypophysial commissure in Myxine and the cartilaginous complex that, in Selachii, divides the polar fenestra into two parts (the hypophysial and the anterior basicranial fenestra). In these animals the carotid arteries run into the cranial cavity caudally to these structures. However, the homologization of these vessels in the various groups seems doubtful (cf. ALLIS 1923—24 b). Further, the naso-hypophysial tube in Myxine runs dorsally to the hypophysial commissure.

In Selachii the polar cartilage portion of the trabecle is short. In Petromyzon it is comparatively longer, and the commissure fuses with its caudal part. In Myxine it also seems to be fairly long, while the hypophysial commissure probably fuses with its rostral part (HOLMGREN 1946). Thus, in Myxine, the part of the trabecle that lies rostrally to the hypophysial commissure would correspond to the part of the trabecle that, in Gnathostomes (HOLMGREN 1946) and Petromyzon, develops in the premandibular somite. The trabecular commissures in Gnathostomes and Petromyzon seem to be homologous. Should HOLMGREN's interpretation, that the trabecular commissure in the Myxine embryo is homologous with the trabecular commissure of Gnathostomes, be correct, it would be homologous also with the trabecular commissure in Petromyzon.

HOLMGREN (1946) has also suggested that the pedicle process might be a basi-trabecular process. To judge from the position of this element only, this

seems reasonable, as this process fuses with the part of the trabecle that, obviously, is to be regarded as homologous with the polar cartilage part in Selachii. However, the development does not suggest that it is formed as a process from this part. As stated by DAMAS (1944), it forms independently in the adjacent ectomesoderm. If this is correct, the process in question should, apparently, in the first place be considered as a visceral formation.

In Gnathostomes, a portion of the lamina basiotica connects the polar cartilage and the parachordal cartilage (HOLMGREN 1940, 1943 a). The same appears to apply to Myxine (HOLMGREN 1946). In Petromyzon the parachordalia develop from the sclerotomes of the 3rd—5th segments (DAMAS 1944), and fuse directly with the caudal end of the trabecles. Laterally, the parachordal cartilage is connected with the auditory capsule by means of a basiotic process. In this respect Myxine seems to resemble Gnathostomes more than Petromyzon.

2. THE VISCERAL ELEMENTS OF THE CRANIUM.

As early as in 1832, RATHKE suggested that the branchial arches of Petromyzon were homologous with the extrabranchialia in sharks. BALFOUR (1881) expressed the same opinion. However, HUXLEY (1875—76), PARKER (1883) and HOWES (1891—92) considered that the visceral arches in Cyclostomes and Gnathostomes were homologous. DOHRN (1884) tried to show that the superficial position of the branchial arches of Petromyzon, as compared to those of sharks, was to be regarded as a secondary phenomenon and that, consequently, no objection could be raised to a homologization. Against DOHRN's opinion, GOETTE (1901) stated that the branchial arch of Petromyzon fundamentally differs from that of Gnathostomes on account of the from its origin superficial position. SEWERTZOFF (1916—17) endeavoured to trace the origin of Gnathostomes and Cyclostomes back to a common ancestor. Both these groups should, according to SEWERTZOFF, have developed the peculiar features of their system of branchial arches independently and, for this reason, the arches should be regarded as directly comparable. NEUMAYER (1938) agrees with SEWERTZOFF in this respect. ALLIS (1923—24) tried to homologize cranial elements in Cyclostomes with extra-visceral elements in Gnathostomes, on the assumption that, in all groups of animals, trabecles and polar cartilages are pharyngeal elements in the premandibular and mandibular segments, respectively. DAMAS (1944) stated that, on account of embryological facts, the branchial arches of the two groups were not homologous. Recently, HOLMGREN (1942, 1943 a, b, 1946) has been able to show that internal as well as external arches may exist in an embryo of Myxine and, probably, also in Petromyzon.

Comparisons between the two recent groups of Cyclostomes were made by MÜLLER (1834), PARKER (1883), HOWES (1891—92), NEUMAYER (1898, 1938), ALLIS (1903, 1923—24 b) and HOLMGREN (1942, 1943 a, b, 1946).

In comparisons between Cyclostomes and Gnathostomes, Petromyzon does not, as far as the visceral formations are concerned, constitute a suitable material. The visceral elements in Petromyzon are almost exclusively extrabranchial. This is obvious from the fact that they are situated laterally to the nerves and vessels pertaining to them. However, HOLMGREN (1946) has pointed out that the anterior lateral cartilage lies medially to the nervus trigeminus II and borders on the medial mucous membrane in the body wall. This would, in his opinion, indicate that there is a question of a real internal arch. Because of its position it is regarded as premandibular. During metamorphosis, this cartilage element develops medially to the part that may, possibly, be the homologue of a premandibular external arch (p. 255). It forms in a blastema which originates from the thickened connective tissue that borders on the medial mucous membrane of the body wall. Its position may justify the interpretation of this formation as belonging to the premandibular segment. The metamorphic development suggests that the structure may earlier have been more important than at the present time. The blastema forms early during metamorphosis, and is considerably larger than the cartilage element it gives rise to. Besides, it changes into cartilage very late. These observations indicate that the peculiar duplication of the primordia of the branchial arches, described by HOLMGREN in Myxine (1942, 1946), may also appear in Petromyzon.

A similar duplication may, possibly, be traced in the mandibular segment. Here, also connective tissue, situated between the muco-cartilage of the ventrolateral plate and the medial mucous membrane of the body wall, takes part in the formation of the cartilage in the adult. In this case, the processus styliformis, with the cornual cartilage, is concerned. HOLMGREN compares the latter with the dental plate in Myxine which may, perhaps, be homologous with the mandibular complex in Holocephali and Antiarchi. In Myxine, as well as in Petromyzon, these formations are penetrated by branches of the nervus trigeminus. However, a considerable difference exists in the fact that the nerve, which in Myxine penetrates the cartilage from the ventral side, is a sensory branch, while in Petromyzon, as communicated by HOLMGREN to the author, it contains only motor fibres, penetrating the cornual plate from the dorsal side. As to the cornual plate HOLMGREN has later (1946) expressed doubts about these attempted homologizations. Nevertheless, it is an important fact that parts of both the skeletal elements in question lie medially to the nerve belonging to them. At present, however, this circumstance does not allow any exact definition of the nature of the cornual plate.

As regards the other arch elements in Petromyzon, there is no reason to suppose the existence of internal arches. True, DAMAS (1944) states that connective tissue of ectomesodermal origin follows the branchial vessels but, as far as can be seen, there is, in these regions, no indication of a development of skeletal elements.

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HOLMGREN (1942) has compared the dorsal labial cartilages in certain sharks and Holocephali and the rostral dorsal cartilages in Petromyzon. This comparison, characterized by HOLMGREN as very hypothetic, is based, inter alia, on a supposition by SEWERTZOFF (1916—17) that the anterior and posterior labial cartilages in Selachii correspond to the posterior lateral cartilage and the vertical part of the subocular arch in Petromyzon. HOLMGREN (1943 a) has later altered his opinion on this question and suggested that the subocular arch in Petromyzon may be homologous with the lamina orbitonasalis + the antorbital cartilage in Heptanchus.

It will seem that at least two of HOLMGREN's suggestions may be confirmed by what happens in the course of the cranial metamorphosis in Petromyzon. Thus, HOLMGREN assumes that "the buccal part" of the skull of Petromyzon has originally been shorter. The extension rostrad of this part does not take place until late during metamorphosis, simultaneously with the final breaking-down of the surrounding tissue. This fact may, possibly, serve as a reason for an assumption that this growth rostrad is only secondary. HOLMGREN tries also to homologize the posterior and anterior dorsal cartilage in Petromyzon with certain binary formations in Holocephalians (prelabial cartilage and prenasal cartilage, respectively). At least the anterior dorsal cartilage is primarily formed during the metamorphosis as a binary primordium. In Petromyzon the cartilage elements lie rostrally to the nasal aperture, but in Holocephalians the elements in question are situated laterally or caudo-laterally. The reversals in the relation between the nasal sac and the cartilage elements in question, in the two objects of comparison, are, apparently, more easily explainable if the cartilages concerned in Petromyzon have originally been binary formations, as, in fact, suggested by HOLMGREN.

The present investigations on Petromyzon do not seem to add any new arguments to the homologies established by HOLMGREN (1942, 1943 a, b, 1946). As stated by HOLMGREN (1942), nothing but a deeper knowledge of the embryonic development of Holocephalians could shed further light on these problems.

The earliest attempts at establishing homologies between the cranium of Myxine and that of Petromyzon rest, as a rule, on a very slight foundation. The most obvious difficulty has been caused by the lack of data regarding the formation and development of the cranium of Myxine. Recently, however, NEUMAYER (1938) and HOLMGREN (1942, 1943 b, 1946) have contributed to the establishment of a sounder basis for these comparisons, inter alia through their descriptions of certain stages in the cranial development of Bdellostoma and Myxine, respectively. Unfortunately, essential points of the development still remain obscure. Thus, nothing is as yet known regarding the origin of the various primordia. NEUMAYER has devoted a particular study to such skeletal primordia as have already been formed into cartilage or procartilage. As

stated by HOLMGREN (1946), several, as yet but mesenchymatic, primordia have in this way, no doubt, escaped sufficient study. HOLMGREN (1946) has paid particular attention to these blastematic primordia in his Myxine embryo, inter alia because of the fact that, at that stage, they formed a preponderant part of the future cranium. A reconstruction of such primordia, without access to the following stages, must be most difficult. This will be evident from a comparison between the pictures first published by HOLMGREN (1942) and the final ones (1946). There are certain, though minor, differences. Below, attention will be directed only to the results published more recently.

Provided that the cartilage skeletons in Petromyzon and Myxine, which are built of slender bars, are remains, deriving from a reduction of—perhaps, fairly dissimilar, but, in both cases, well developed—skulls, a certain hesitation, with regard to the result of a comparison between these objects, is unavoidable. To this has to be added that the skulls of Petromyzon and Myxine—in accordance with a general opinion—seem to have been secondarily adapted to their function. HOWES (1891—92) attempted a homologization between the crania of Bdellostoma and Petromyzon, proceeding, it will seem, from an assumption that practically every part in one of these animals would necessarily correspond to some part in the other. Strangely enough the equation almost balanced. The explanation is that the number of cartilaginous elements in both these animals is nearly the same. The slight actual differences in number were interpreted as due to the disappearance of homodynamic elements. This applies, inter alia, to certain branchial arches in Myxine.

NEUMAYER'S (1938) comprehensive attempt at establishing homologies between Petromyzon and Bdellostoma are far better founded than HOWES'. Relations to other organ systems have been thoroughly analysed. Unfortunately, NEUMAYER'S work is, partly, rather selfcontradictory. The interpretation of the nerves is various. Also, his statements lack clearness with regard to the skeletal elements (cf. HOLMGREN 1942), a fact, probably, to be explained by NEUMAYER'S death before the publication. NEUMAYER, also, adopts SEWERTZOFF'S (1916—17) interpretation of the Petromyzon cranium, already criticized in the light of the results arrived at in this investigation, and, also, with reference to objections raised by HOLMGREN (1946).

HOLMGREN (1946) itemizes his opinion of the homologies between Petromyzon and Myxine as follows:

1. "All arches in Petromyzon are external." This opinion has been accepted by the present author, yet, with reference to the statements above regarding the anterior lateral cartilage and the cornual cartilage.

2. "There are in Myxine external as well as internal (true) arches."

3. "The dorsal series of longitudinal bars in Petromyzon represent basal parts of external arches." The term "basal parts" seems, in HOLMGREN'S

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sense, to be the equivalent of the subchordal longitudinal bar. On this point, the opinion of the present author differs. For reasons previously stated (see Chapter V), the subocular arch and the connection between the processus styliformis and the extra-hyal have been interpreted either as a dorso-lateral longitudinal bar or, possibly, as an epitrematic one, as suggested by SEWERTZOFF. In the present investigation, the dorsal caudally directed process on the extra-hyal has been interpreted as a remainder of a dorso-lateral longitudinal bar situated in this spot.

4. "In the prebranchial part of the visceral skeleton no epi- or hypotrematic bars are present in Petromyzon, nor in Myxine." As regards Petromyzon, the previous paragraph should be referred to. No hypotrematic elements seem to exist rostrally to the extra-hyal.

5. HOLMGREN states that the trabecular commissure in Petromyzon is surrounded by a cartilaginous mass which, laterally, fuses with the vertical part of the subocular arch. This latter part HOLMGREN terms "anterior pillar". "The anterior pillar of the subocular bar may perhaps correspond to the short transversal cartilage bar, which connects the dorsal longitudinal bar with the trabecula in Myxine, and the commissural part with the commissure of the longitudinal bars in the Myxine embryo." The fusion of the dorsal longitudinal bar with the trabecle in Myxine is considered by HOLMGREN to be of a "trabecular origin". In view of the fact that, in addition, it lies caudally to the point of fusion of the hypophysial commissure with the trabecle in the Myxine embryo, it seems rather doubtful if the anterior pillar actually corresponds to the forementioned bar in Myxine.

Since "the commissure in the longitudinal bar" in the embryo gives rise to the palatine bar in the full-grown Myxine, this bar is also the homologue of the commissural part in Petromyzon. This, however, does not appear from HOLMGREN's survey (1946, p. 33). But if this commissure is homologous with the cartilaginous parts that rostrally unite the subocular arches in Petromyzon, also the vertical parts of the subocular arches seem to be represented in the rostral parts of the longitudinal bar in Myxine. The connection between the dorsal longitudinal bar and the trabecle in Myxine is binary, while, in Petromyzon, it is single and broadly surrounds the rostral part of the trabecle and the trabecular commissure. Provided that the differences in position, referred to above, are of less importance, the possibility that the homologue of the binary connection in Myxine is to be found within the mentioned region in Petromyzon cannot, it seems, be excluded.

6. The posterior lateral cartilage is homologized by HOLMGREN with the cornual cartilage in Myxine. However, during metamorphosis—as shown in this work—the posterior lateral cartilage and the anterior dorsal cartilage, are formed as one single rostro-dorsally directed blastematic process. Through a

later increase in growth the two primordia of the anterior dorsal cartilage unite in the median line. In the course of this process the single anterior lateral cartilage forms. In Myxine the cornual cartilage is characterized by a broadening of its rostral part. In this way it resembles the common primordium of the posterior lateral and anterior dorsal cartilages in Petromyzon at certain early metamorphic stages. According to HOLMGREN's observations, there are indications that the two primordia of the cornual cartilage in the Myxine embryo are united medially by means of a blastematic commissure. For this reason, the cornual cartilage in Myxine may, in the opinion of the present author, be supposed to be homologous at least with certain parts of both the forementioned cartilage elements in Petromyzon. In fact, they, always keep in a contact with each other.

7. The extra-hyal and the extra-mandibular in Petromyzon are homologized with the first and the second prebranchial arches, respectively, in Myxine. These structures have similar relations to the nervus hyomandibularis VII and the nervus mandibularis V, respectively, in Myxine and in Petromyzon. In both there is a question of external arches.

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8. In Petromyzon the nervus trigeminus II, a branch of the nervus suborbitalis, which contains sensory as well as motor fibres, runs medially to the posterior lateral cartilage (as well as medially to the anterior dorsal cartilage, a fact that should be kept in mind), but laterally to the anterior lateral cartilage. In Myxine the nervus trigeminus II runs medially to the cornual cartilage but laterally to the so-called labial cartilage. The latter forms the base of the cartilage elements in the first and third tentacle. From these premises HOLMGREN draws the following conclusions: Firstly, the attempted homologization mentioned in paragraph 6 is confirmed. Secondly, these facts lend support to attempts at homologizing the anterior lateral cartilage in Petromyzon with the labial cartilage in Myxine (cf. below, paragraph 9). Thirdly, the interpretation of these elements as internal premandibular arches is confirmed.

9. HOLMGREN, who (1936) supposed the anterior lateral cartilage to be derived from muco-cartilage in the lateral mouth plate, considers that this structure in the Petromyzon larva is homologous with the labial cartilage in Myxine. As already shown in the present investigation, the anterior lateral cartilage has another origin and, consequently, HOLMGREN's opinion does not seem probable. HOLMGREN also suggests that the basal plates in Myxine should correspond in Ammocoetes to the ventro-lateral plate which, like the basal plates in Myxine, have "relations to the external visceral arches". But HOLMGREN suggests another interpretation, "probably a better way of explaining the basal skeleton of Myxine on the basis of the conditions in Petromyzon. The basal skeleton in the Myxine embryo consists of three segments, of which the

foremost is composed of two skeletal plates on each side, the middle of a paired and the caudal of one unpaired piece. In Petromyzon the lingual skeleton likewise consists of three segments, of which the anterior comprises four pieces whereas the others are unpaired. The two foremost segments are quite short, situated in the 'tongue', the hindmost is very long, forming the lingual cartilage." Here it should be added that the labial cartilage in Myxine connects with the anterior, binary segment of the basal plate by means of a cartilaginous bar. In Petromyzon a blastema is formed connecting the blastema in the "tongue" with the primordium of the anterior lateral cartilage. In the view of the present author, this fact verifies the comparisons made by HOLMGREN. In the larva, the piston cartilage is represented by the muco-cartilage in the ventro-medial longitudinal bar, while the cartilage in the "tongue" develops from the connective tissue in the medial tentacle of the larva. Therefore, HOLMGREN's first-mentioned attempts at homologization of larval elements seem less probable.

Further, HOLMGREN considers the velar skeletons in Myxine and Petromyzon as homologues. In both animals these structures lie medially to the nerves. However, the velar skeleton in the Myxine embryo fuses, dorso-rostrally, with the medial side of the "extra-palatoquadrate". In the larva of Petromyzon the velar skeleton fuses with the ventral side of the trabecle, while the commissure serves as an intermediary. In young larvae, an easily observable mesenchymatic mass runs latero-caudally from the velar skeleton towards the pedicle process. Therefore, a connection between the velar skeleton and the extra-mandibular arch seems to exist also in Petromyzon. Still, in the adult Petromyzon the velar skeleton is not connected with other, dorsal skeletal elements. In the beginning metamorphosis, the blastema of the velar skeleton forms dorsally in the muco-cartilage but, in the course of metamorphosis, this primordium moves more and more ventrad.

In the following table a summary is given of the above discussed possibilities of homologization in the cranium of Petromyzon and Myxine:

Petromyzon	Myxine
Neural skeleton	
Parachordals[1]	Parachordals
Trabecle[1]	Trabecle
Trabecular commissure[1]	Trabecular commissure (in embryo)
Muco-cartilaginous commissure (in larva)	Hypophysial cartilage
Auditory capsule	Auditory capsule
(Processus basiotica?)	Lamina basiotica
Nasal capsule[1]	Nasal capsule

[1] HOLMGREN (1946)

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Petromyzon	Myxine
Visceral skeleton	
Dorsal, longitudinal part of extra-hyal + subocular arch(1)	Dorsal longitudinal bar
Cartilage connecting vertical parts of subocular arches	Palatine bar (+ rostral connection between dorsal longitudinal bar and trabecle?)
Extra-hyal[1]	Extra-hyal
Extra-mandibular[1]	Extra-mandibular
Cornual plate[1]	Toothplate cartilage (?)
Lateral mouth plate (in larva)	
Anterior lateral plate[1]	Labial cartilage
Posterior lateral plate + anterior dorsal plate	Cornual cartilage
Posterior dorsal plate[1]	Subnasal cartilage
Velar skeleton(1)	Velar skeleton
Lingual cartilages[1]	Basal plates
Annular cartilage Stylet cartilage Medial ventral plate	

[1] HOLMGREN (1946)

In the above list some skeletal elements in the adult Myxine, as well as in the embryo, are omitted.

VII. A COMPARISON BETWEEN PETROMYZON AND CEPHALASPIDS.

As early as in 1900, GASKELL homologized the muco-cartilaginous complex in the Petromyzon larva with certain skeletal elements in Cephalaspids. STENSIÖ (1927, 1932), who has contributed largely to our knowledge of the structure of Cephalaspids and other Ostracoderms, has compared in detail the organ systems of Cephalaspids and Petromyzon. In Cephalaspids the voluminous endoskeleton was more or less completely ossified, and to a great extent surrounded other organs. Since the ossified parts remain after the fossilation process, STENSIÖ was able to describe many anatomical details. In other Ostracodermi the endoskeleton is unknown but, according to STENSIÖ, it should have resembled that of the Cephalaspids, though no ossification had taken place. The relationship between Ostracoderms and Cyclostomes appears to be a well documented fact. Lately, however, WHITE (1946) has suggested the possibility of other evolutionary courses.

In comparing Cephalaspids and Petromyzon, STENSIÖ proceeded from facts, recorded by HOLMGREN and others, in the larva of Petromyzon. The reason

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for choosing the larva as the object of comparison was, inter alia, that the muco-cartilaginous skeleton is as extensive as to be compared with the endoskeleton of Cephalaspids. In the full-grown Petromyzon, the cartilaginous cranium has an entirely different character. It should, however, be noted that the cartilaginous elements in the larva have also been supposed to possess homologues in the endoskeleton of Cephalaspids. HOLMGREN and STENSIÖ (1936, p. 286) summarize the relations between the cranium in the larva of Petromyzon and that of the full-grown animal as follows: "Die Metamorphose der Petromyzonlarve besteht somit einerseits in Abwerfung von larvalem Skelettgewebe und andererseits in Ausnutzung anderer Teile desselben Gewebes. Durch die Metamorphose verliert das Skelett vollständig seinen Charakter einer zusammenhängenden, die Organe infiltrierenden Skelettmasse und bildet sich zu einem Skelett aus von einander wohlbegrenzten einzelnen Skelettstücken um. Spiegelt das Skelett der Petromyzonlarve phylogenetisch ältere Zustände wieder, so dürfte das Kopfskelett der Vorfahren eine kompakte Skelettmasse gewesen sein, durch die die Nerven und Gefässe hindurchtraten. Die Verhältnisse des Schleimknorpels deuten folglich an, dass sich die Petromyzonten unter den Ostracodermen den Cephalaspiden anschliessen."

Provided that the ancestors of Petromyzon—like Ostracoderms—were once in the possession of a continuous endoskeleton, it seems safe to assume that the larva of Petromyzon in this respect represents a more primitive state than the full-grown animal. The cartilaginous cranium is supposed to be secondarily adapted to special functions. On the other hand, it has been previously suggested, in the present investigation, that various facts concerning the origin and the development of muco-cartilage and cartilage indicate that muco-cartilage from evolutionary point of view is a younger tissue than cartilage. This would signify that the full-grown animal is primitive with regard to the skeleton material, while the larva should be more primitive in so far as the skeleton morphology otherwise is concerned. Nevertheless, muco-cartilaginous elements are in no way excluded as a basis for morphological discussions. The present investigation has, rather, added material to the opinion that a genetic connection between muco-cartilage and cartilage exists. It is, however, essential to observe that also larval connective tissue of another type than muco-cartilage may change into cartilage during metamorphosis. Also such tissue may, therefore, be assumed to have homologues in the endoskeleton of Cephalaspids. In addition, Petromyzon shows a more pronounced tendency towards cartilage formation than the extent of definitive cartilage elements in the full-grown animal would seem to indicate. This tendency is manifested, in the larva, by the presence of aberrant cartilage elements and, during metamorphosis, by the formation of blastemas connected with and, apparently, histologically identical with the real cartilage blastemas, without, however, giving rise to any cartilage.

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As previously stated (see Chapter III), HOLMGREN and STENSIÖ (1936) have drawn the conclusion, from their investigations on the larva of Petromyzon, that the muco-cartilage has a very extensive distribution. They examined young larvae and pointed out that, at later stages of development, certain parts of the muco-cartilage complex will be pushed aside, because of the development of the organs, chiefly musculature. From what is said in chapter III it is evident, however, that muco-cartilage in the proper sense does not seem to have the extension suggested by HOLMGREN and STENSIÖ. Within large areas, other types of connective tissue are to be found. However, during metamorphosis, this tissue will partly change into cartilage. In view of these circumstances, HOLMGREN's and STENSIÖ's observations, on the relations between the connective tissue complex, on one hand, and vessels, nerves and musculature, on the other, still seem to be relevant. This also applies to their homologization of this connective tissue complex in the larva of Petromyzon with the endoskeleton of Cephalaspids.

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Recently, DAMAS (1944) has compared the distribution of ectomesoderm, at certain embryonic stages in Petromyzon, and the endoskeleton of Cephalaspids. DAMAS considers that in this way a more complete material for an attempt of homologization will be obtained than that available to HOLMGREN and STENSIÖ from their study of the distribution of muco-cartilage only. However, DAMAS' criticism loses in value in view of the fact that HOLMGREN and STENSIÖ have based their observations on young larvae of Petromyzon. As stated above, the tissue that, in this connection, has been termed muco-cartilage should, to a fairly large degree, correspond to what DAMAS calls ectomesoderm. Nevertheless, DAMAS has opened up new and interesting perspectives by the careful embryological analysis on which he builds his conclusions.

DAMAS states that the ectomesoderm develops dorsally and ventrally in Petromyzon. While the dorsal ectomesoderm extends along the entire animal, and gives rise, inter alia, to the sheaths of the nervous system, the ventral ectomesoderm is formed solely in the head, for which it is, consequently, typical. Here it changes into cartilage, muco-cartilage and connective tissue, the latter, inter alia, following the branchiomere blood vessels. DAMAS points out that the ectomesoderm, which at late embryonic stages remains as a continous complex, is afterwards pushed aside by other primordia, chiefly of musculature (cf. HOLMGREN and STENSIÖ's statements regarding "muco-cartilage" above).

Thus, the ectomesoderm in the embryo of Petromyzon constitutes a rather complicated system of various primordia. To use such a material for comparisons with organs that are known only from adult animals, as in the case of the endoskeleton of Cephalaspids, seems, for this reason, a fairly hazardous procedure. It is possible that, also in Cephalaspids, the ectomesodermal component has, to some extent, differentiated into various kinds of connective tissue, as happens in Petromyzon. For natural reasons, our knowledge of the distribu-

tion of the various types of supporting tissue in this fossil material is very incomplete. This applies, especially, to the ventral parts.

To the present author it seems not unlikely that DAMAS has underrated the significance of the entomesodermal components in the cranial skeleton of Cyclostomes. In Petromyzon, they play an important part in the neural cranium, a more important one, probably, than DAMAS has ascribed to them, and, also in Cephalaspids, entomesodermal components are likely to have formed part of the endoskeleton. True, the parts corresponding to trabecles, parachordalia and auditory capsules are not distinguishable in the endoskeleton complex of Cephalaspids, which does not mean that they have not been developed. In the cranial basis, entomesoderm and ectomesoderm form, as a rule, continuous skeletal structures in Vertebrates.

Earlier, it has been suggested that muco-cartilage should represent a primitive tissue (GASKELL 1900, TRETJAKOFF 1927 c, 1929 a, STENSIÖ 1927, 1932, HOLMGREN and STENSIÖ 1936). It has also been assumed to form part of the endoskeleton in Cephalaspids. In the case of Petromyzon, the only animal in which muco-cartilage has actually been observed, it seems most likely that cartilage has been of a greater significance, phylogenetically, than muco-cartilage. It should be added that, while ossification of the endoskeleton as a rule passes through an initial stage of cartilage, there is no known instance of ossification in connection with muco-cartilage. In certain Cephalaspids (Boreaspis rostrata, STENSIÖ 1927) the endoskeleton was ossified, even though, as a rule, only perichondrial ossification, or none at all, is described in Ostracodermi.

The interbranchial septa in the oro-branchial chamber in Cephalaspids have been homologized by STENSIÖ with external branchial arches, which, according to SEWERTZOFF (1916—17), are partly represented by muco-cartilaginous structures in Petromyzon. As previously stated, STENSIÖ is of the opinion that only one premandibular arch has existed in Cephalaspids. He homologizes this arch with the lateral mouth plate in the larva of Petromyzon. In the present investigation, further reasons have been advanced for the opinion that the lateral mouth plate constitutes such an arch, or rest of an arch.

STENSIÖ (1927) points out that the part of the visceral endoskeleton ventrally to the gill openings in Ostracodermi is completely unknown. He writes (p. 144) as follows: "Owing to its position in the ventral wall of the oralo-branchial chamber, that certainly was intensely moved and played an important part for the respiration, the ventral division must either have been a single thin big plate of some flexible sort of cartilage or have consisted of a number of small independent cartilaginous plates." In some Cephalaspids the oro-branchial fenestra was covered by many small exoskeletal plates. The arrangement of these plates does, however, not suggest anything regarding the shape of the underlying endoskeletal formations.

The skeletal tissue in the oro-branchial fenestra is homologized by STENSIÖ

with the portion of the ventro-lateral plate in Petromyzon between the ventral longitudinal bars in and rostrally to the branchial basket. The fact is also stressed that, after metamorphosis, the branchial basket in Petromyzon loses much of its "cephalaspid-like" character, as the ventral longitudinal bars fuse ventrally with one another in the median line.

However, to some extent, this comparison seems to halt. The part of the branchial basket of Cephalaspids, about which little is known, presumably, because it consisted of less resistant tissue, was situated ventrally to the gill slits. For this reason, the corresponding part in Petromyzon—the larva as well as the adult animal—should, it seems, include also the hypotrematic parts of the cartilaginous branchial arches.

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SUMMARY.

1. The histological structure of muco-cartilage has been examined. Muco-cartilage seems to consist of a network of branched cells, surrounded by intercellular substance. The fibroid elements in muco-cartilage are formed by cell processes. The staining reactions of the latter are different from other types of connective tissue. The cell nucleus is surrounded by an "endoplasm" which stains differently from the "ectoplasm" outside it. The double refraction which has been observed in the cell processes seems to depend upon properties of the "ectoplasm". The shape of the cell processes varies considerably within one and the same muco-cartilaginous complex, as well as from one complex to another. The intercellular substance reveals staining reactions suggestive of the matrix in cartilage (SCHAFFER 1896) and embryonic mesenchyma. During the ontogenetic development muco-cartilage differentiates very slowly (Chapter III, 1).

On account of the origin and development of muco-cartilage and cartilage, during ontogeny and metamorphosis, it is suggested that muco-cartilage is, possibly, a secondary larval tissue and that cartilage has, probably, had a larger distribution in the cranium during earlier phylogenetic stages than at present (Chapter V, 1).

2. The elements of fibrous connective tissue, muco-cartilage and cartilage in the larval cranium are described. The existence of a muco-cartilaginous commissure between the trabecles, on a level with the medial velar skeleton, has been described. Certain aberrant cartilage structures, outside the normal area of distribution of this tissue, have been observed (Chapter III, 2).

3. The trabecles are, primarily, formed in the sclerotomes of the first and second segments. The trabecular commissure is, probably, of ectomesodermal origin, and changes into cartilage independently of the trabecles. The devel-

opment of the medial velar skeletons, and of the commissure between the trabecles, on a level with these structures, is described (Chapter III, 3).

4. The metamorphosis of the head skeleton has been studied. Cartilage is formed, partly from muco-cartilage, partly from other connective tissue. The former process is studied also from a histological point of view. Accounts are given of the breaking-down, and disappearance, of muco-cartilage. The development of the various cartilaginous elements in the full-grown animal is described. A summary of this developmental process is submitted (Chapter IV, p. 235).

5. The homologies of different parts in the larval and the adult crania, respectively, are discussed. In this connection the question of the existence of prebranchial arch elements in Petromyzon is dealt with (SEWERTZOFF (1916—17). Like STENSIÖ (1927), and others, the present author considers that three more or less complete prebranchial arches can be distinguished in these animals, the first one being the extra-hyal in the full-grown animal, which, essentially, has the shape of an ordinary external branchial arch. For certain reasons, the styliform cartilage has been supposed to represent an extra-mandibular. During metamorphosis, the blastema of this structure develops in such a way as to render a ventral connection with the ventral longitudinal bar in the extra-hyal probable. Later, this blastematic connection disappears without leaving any further key to its nature. The development of the remaining dorsal parts is very complicated. The fully developed styliform cartilage is very different to a normal branchial arch. The extra-premandibular arch is supposed to be represented by the lateral mouth plate in the larva. At the base of this structure, aberrant cartilage has developed within the muco-cartilage in two different specimens, a fact which has been considered to lend support to the hypothesis mentioned above. During metamorphosis, the lateral mouth plates disappear without forming any cartilaginous element. For this reason, an extra-premandibular is supposed to be missing in the adult. Possibly, a real internal premandibular arch may be represented by the anterior lateral cartilage (HOLMGREN 1946).

In the adult there are certain longitudinal cartilaginous elements in the prebranchial region. They have been interpreted as rostral extensions of some of the longitudinal bars developed in the branchial region (Chapter V, 2).

6. The trabecles in Petromyzon and those in Gnathostomes agree, particularly with regard to their origin. This is, however, as far as Myxine is concerned, but little known. The previously mentioned muco-cartilaginous commissure between the trabecles has been homologized with certain cartilage elements in the polar fenestra in Selachians. Earlier these Selachian elements have been homologized by HOLMGREN (1946) with the hypophysial commissure in Myxine. The origin and development of the parachordalia are discussed (Chapter VI, 1).

7. A comparison between the visceral elements in Petromyzon and Myxine, and, to some extent, also in Gnathostomes, has been carried out. The results of the homologizations between Petromyzon and Myxine have been assembled in a table on pages 266—267 (Chapter VI, 2).

8. The possibility of homologizing the skull of Petromyzon with the Cephalaspid cranial endoskeleton is discussed (Chapter VII).

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ABBREVIATIONS.

ab.c. aberrant cartilage structure.
a.car. arteria carotis.
a.d.p. anterior dorsal plate.
a.d.p.r. anterior dorsal plate primordium.
a.fac. arteria facialis.
a.hy. arteria hyoideus.
a.l. arteria lingualis.
a.l.ap. anterior lateral apical cartilage.
a.lat.p. anterior lateral plate.
a.ling. arteria lingualis.
a.mand. arteria mandibularis.
an.c. annular cartilage.
an.c.r. annular cartilage primordium.
ao. aorta dorsalis.
bl. blastema.
bl.v.l.p. blastema in the ventro-lateral plate.
br.1. 1:st branchial arch.
b.v. blood vessel.

c. cartilage.
c.b.c.f. cartilage in the basi-cranial fenestra.
ch. notochord.
com. commissure.
corn.p. cornual plate.
c.t. connective tissue.
c.t.bl. blastema developed in connective tissue.
d.l.bl. dorso-lateral blastema.
e. eye.
e.l.b. epitrematic longitudinal bar.
e.mes. ectomesoderm.
ent. entoderm.
ex.hy. extra-hyal.
ex.hy.bl. extra-hyal blastema.
f.a.fac. foramen for arteria facialis.
f.n.p. foramen for nervus perforans.
g.V. ganglion trigeminus (V).
g.VII. ganglion facialis (VII).
g.IX. ganglion glossopharyngeus (IX).
gut. intestine.
h.l.b. hypotrematic longitudinal bar.
l.ap.c. lateral apical cartilage.
lat.w. lateral wall of brain capsule.
l.m.p. lateral mouth plate.
l.v.sk. lateral velar skeleton.
l.w. lateral wall of brain capsule.
m. mesenchyma.
m.ap.c. medial apical cartilage.
m.bas. musculus basilaris.
m.buc. musculus buccalis.
m.c. muco-cartilage.
m.c.a. musculus cardio-apicalis.
m.c.bl. blastema in muco-cartilage.
m.d.l.s. musculus depressor labii superioris.
m.mand.p. musculus mandibularis posterior.
m.m.g. musculus mandibulariglossus.
m.ph. musculus pharyngeus.
m.s.l. musculus sublabialis.
m.t. medial tentacle.
m.v.c. medio-ventral cartilage.
m.v.h. musculus velohyoideus.
m.v.sk. medial velar skeleton.
n.hy. nervus hyoideus (VII).
n.mand. nervus mandibularis (V).
n.per. nervus perforans (V).
n.s.o. nervus suborbitalis (V).
n.sup.o. nervus supraorbitalis (V).
olf.c. olfactory capsule.
ot.c. otic capsule.
p.c. parabuccal cell band.
p.ch. parachordal.
p.d.p. posterior dorsal plate.
ped. pedicle.
pist.c. piston cartilage.
p.lat.p. posterior lateral plate.
pro.c. procartilage.
r.d.p. rostro-dorsal plate.
seg.2. 2:nd segment.
s.l.b. subchordal longitudinal bar.
s.oc.a. subocular arch.
s.oc.m.c. subocular muco-cartilage portion.
s.ot.bl. subotic blastema.
s.ot.c. subotic cartilage part of extra-hyal.
s.ot.m.c. subotic portion of muco-cartilage.
st.c. styliform cartilage.
st.c.bl. styliform cartilage blastema.
sty.c. stylet cartilage.
sty.c.r. stylet cartilage blastema.
t. trabecle.
t.com. trabecular commissure.
th.b.o.c. thickened bar of orbital capsule.
t.r. trabecle primordium.
vel. velum.
v.l.b. ventral longitudinal bar.
v.l.p. ventro-lateral plate.
v.m.l.b. ventro-medial longitudinal bar.
v.s. vesicular supporting tissue.
v.sk. velar skeleton.
x. limit of original extension of muco-cartilage.
1. Cartilage processes on branchial arches.
2. Cartilage processes on branchial arches.
3. Cartilage processes on branchial arches.

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ÜBER DIE ENTWICKLUNG UND MORPHOLOGIE DES CHONDROCRANIUMS VON PROCAVIA CAPENSIS PALL

VON

PER ERIC LINDAHL

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EINLEITUNG.

Die primitive Ungulatenordnung Hyracoidea hat durch ihre systematische Stellung grosses Interesse erregt. Um so mehr ist es zu verwundern, dass die Embryologie dieser Tiere nicht Gegenstand zahlreicher Untersuchungen geworden ist. Die Entwicklung des Schädels ist bis jetzt nirgends eingehend behandelt worden. Allerdings wurde das Chondrokranium von „Hyrax procavia" von FAWCETT, LLEWLYN und DOBSON modelliert und 1927 bei einer Sitzung der Association des Anatomistes in London demonstriert; es sind jedoch weder Beschreibung noch Abbildungen erschienen. Die einzigen Arbeiten, die die Entwicklung des Schädels von Procavia betreffen, beschäftigen sich nur mit dem Entotympanicum (PARKER 1874, Fussnote S. 319, VAN DER KLAAUW 1922).

Da mir ein sehr schönes embryologisches Material von Procavia capensis zur Verfügung stand, habe ich in der vorliegenden Arbeit das Chondrokranium dieser Art und seine Entwicklung untersucht. Allerdings äussert DE BEER (1937) folgende wenig ermunternde Ansicht: „The problem of the relative affinities of the various orders of Placental Mammals is one on which the study of the development of the skull can unfortunately throw but little light...". Es scheint mir jedoch nicht unmöglich, bei Untersuchungen dieser Art die Arbeitsweise der traditionellen Forschungsrichtungen zu erweitern. Diese stellt vor allem vergleichend fest, ob dieses oder jenes Element vorhanden ist oder nicht, wobei es sich um verhältnismässig grosse Einheiten handelt. Da das Chondrokranium allem Anschein nach bei den Mammalia eine regressive phylogenetische Entwicklung durchmacht, die sich in den verschiedenen Ordnungen verschieden gestaltet, dürfte es nicht weniger von Gewicht sein, die Morphologie nicht zurückgebildeter Elemente eingehend zu vergleichen. Von dieser Vorstellung als Arbeitshypothese ausgehend habe ich mich bemüht, das voll ausgebildete Chondrokranium auch in Einzelheiten möglichst vollständig darzustellen, und es wäre von diesem Gesichtspunkt aus sehr wünschenswert, einen Vergleich zwischen einander nahe stehenden Formen anzustellen. Die Entwicklung der verschiedenen Teile des Schädels läuft asynchron ab, und zwar in wechselndem Masse bei verschiedenen Arten und Ordnungen. Folglich kann nur der Entwicklungsmodus, nicht aber die während der Entwicklung auftretende Form Gegenstand eines Vergleiches werden. Da sowohl Proportionen wie Formen auch nachdem die Verknorpelung des Schädels in grossen Zügen durchgeführt worden ist bis zur Erreichung der vollen Entwicklung stark verändert werden können, sollten zu Vergleichen dieser Art nur beinahe oder ganz voll entwickelte Stadien herangezogen werden.

ÜBER DAS CHONDROKRANIUM VON PROCAVIA CAPENSIS

Herrn Professor NILS HOLMGREN, der mir ursprünglich das wertvolle Material zur Verfügung stellte und meine Arbeit in grosszügiger Weise unterstützte, spreche ich hier meinen herzlichen Dank aus. Mein Dank gilt auch Frau Simone Thörnblom, die mir mit der graphischen Rekonstruktionsarbeit und der Ausführung sämtlicher Zeichnungen wertvolle Hilfe geleistet hat.

MATERIAL, METHODEN UND RICHTUNGSANGABEN.

Material: Das reichliche Embryonenmaterial von Procavia capensis des Zootomischen Institutes, Stockholm, ist von Herrn Professor VAN DER HORST (Johannisburg) angeschafft worden. Als Fixierungsmittel kam Bouinsche Lösung zur Verwendung. Bei der vorliegenden Untersuchung habe ich mich Schnittserien folgender Stadien bedient, die mit Azan—Mallory gefärbt worden sind:

Stadium	Scheitel-Steiss-Länge mm	Kopflänge mm	Schnittdicke μ
I	6	2,7	10
II	7	3,6	10
III	9,5	4,4	10
IV	10	5	10
V	12	6	10
VI	12	6,5	10
VII	15,5	7	15
VIII	16,5	8	15
IX	18	9	10
X	19	10	15
XI	22	11	15
XII	33	14	15
XIII	36	16,5	20
XIV	42	20	20

Ein verhältnismässig grosser Teil des Materials lag schon zu Anfang der Untersuchung als Schnittserien mit einer für graphische Rekonstruktion des Schädels ungünstigen Schnittrichtung vor. Es wurden deswegen neue Schnittserien angefertigt. Die Schnittrichtung der frühesten Stadien (I—III) wird in Fig. 1 demonstriert. In den folgenden (IV—V) ist die Schnittrichtung etwa senkrecht zu der in Fig. 1 angegebenen geführt. Im übrigen ist die Schnittrichtung so gewählt, dass sie etwa gleich grosse Winkel mit den ventralen Flächen der Trabekelplatte und der Basalplatte bildet.

In Stadium XII finden sich Knorpelblasteme sehr spärlich und zwar nur in der Ethmoidalregion und hier am Rand der Fenestra narina und an den Turbinalia. Die Cartilago ductus nasopalatini ist hauptsächlich als Blastem vorhanden, und an Schnittserien von Stadien mit Scheitel-Steiss-Länge von 36,

42, 60 und 80 mm konnten noch einige spät erscheinende Knorpelelemente festgestellt werden. Andererseits setzt in Stadium XII an einigen Stellen (Basalplatte, Meckelscher Knorpel) die Auflösung des Knorpels in Zusammenhang mit der Verknöcherung ein. Stadium XII scheint also das „Stadium optimum" zu vertreten.

Methoden: Da sowohl die Plattenrekonstruktionsmethode wie auch das graphische Rekonstruieren mit Mängeln behaftet sind, habe ich vorgezogen, für das Stadium XII, bei dem die feinere Modellierung der Oberfläche von grösster Bedeutung ist, beide Methoden parallel zu benutzen. Mit Ausnahme einiger kleiner Abschnitte ist der ganze Schädel in Sektionen in 33-facher Vergrösserung bei Verwendung jedes zweiten Schnittes modelliert worden. Die graphischen Rekonstruktionen sind hier in 22-facher Vergrösserung mit Verwendung jedes sechsten Schnittes ausgeführt. Projektionen sind von der Seite, von der Medianebene, von ventral und von dorsal dargestellt. Die Übersichtsbilder dieses Stadiums sind graphische Rekonstruktionen, an denen die feineren Einzelheiten und Schattierungen nach dem Wachsmodell ausgearbeitet sind. Von den jüngeren Stadien sind I—VI und IX in 40-facher, die übrigen in 22-facher Vergrösserung graphisch dargestellt. Von den Stadien, die älter sind als das „Stadium optimum" (XII), sind graphische Rekonstruktionen in 20-facher Vergrösserung hergestellt worden. Auch sind manche Einzelheiten wie die weitere Aufteilung des Foramen perilymphaticum und die endgültige Ausbildung der Cartilago ductus nasopalatini modelliert worden.

Hervorzuheben ist, dass alle graphische Rekonstruktionen wiedergebenden Abbildungen Projektionen sind und folglich unperspektivisch, im Gegensatz zu den Abbildungen von Wachsmodellen.

Richtungsangaben wie horizontal, oben, unten usw., die auf einer gewissen mehr oder weniger willkürlichen Lage des Schädels im Raum beruhen, bringen nur Verwirrung und werden vermieden. Als Richtungsebenen werden die Medianebene und die Ebene des Planum basale (ventrale, fast ebene Fläche) verwendet, die senkrecht aufeinander stehen. Bei Angabe des Winkels zwischen irgend einer Linie mit einer dieser Ebenen ist damit der Winkel zwischen der Linie und ihrer Projektion auf die Ebene gemeint. Solche Winkel können also meistens nicht in den Abbildungen nachgemessen werden. Mit dorsoventral wird in jedem Punkt die Richtung bezeichnet, die parallel mit der Medianebene und in einer senkrecht auf dieser und dem ventralen Rand des Schädels stehenden Ebene liegt. Rostrokaudal ist in jedem Punkt die Richtung, die der Medianebene parallel senkrecht auf der dorsoventralen Richtung steht. Die Höhe gibt die Ausdehnung verschiedener Teile in dorsoventraler Richtung an, und schliesslich wird unter Längsrichtung des Schädels die Richtung verstanden, die durch die am weitesten voneinander gelegenen Punkte, Nasenspitze und Tectum posterium, geht.

ÜBER DAS CHONDROKRANIUM VON PROCAVIA CAPENSIS

DIE FRÜHENTWICKLUNG DES PLANUM BASALE.

STADIUM I—III: SCHEITEL-STEISS-LÄNGE 6, 7 UND 9,5 MM, KOPFLÄNGE 2,7, 3,6 UND 4,4 MM, FIG. 1—4.

Zur Feststellung der Anzahl der an dem Aufbau der Occipitalregion teilnehmenden Wirbelaequivalente war es notwendig, Entwicklungsstadien mit einer Kopflänge von 2,7—4,4 mm zu untersuchen. Hier können die Blasteme der Wirbel zum Teil abgegrenzt werden, die Blasteme anderer Knorpelelemente des Kopfes dagegen nicht. Auch die Wurzeln des Nervus hypoglossus tragen wesentlich zum Verständnis der Metamerie der betreffenden Region bei wie auch die metotischen Myotome. Letztere sind schon weitgehend verschmolzen, zeigen aber immer noch genügend freie Teile, um die ursprüngliche metamere Anordnung erkennen zu lassen. Die hier benutzte Schnittrichtung zeigt Fig. 1. Die Myotome, die Wurzel des N. Hypoglossus und die Blasteme der Wirbelelemente sind in Seitenansicht rekonstruiert worden. Zur Erleichterung der Orientierung ist in sämtlichen Abbildungen auch die Chorda eingetragen. An ihr kann die allmählich vor sich gehende Verstärkung der Nackenbeuge verfolgt werden.

Fig. 1. Stad. III. Die Gerade zeigt die für die Stadien I—V benutzte Schnittrichtung.

Das verdichtete Mesenchym, das die Anlage des Skelettes in der Occipitalregion darstellt, bildet in dem Stadium von 2,7 mm Kopflänge eine zusammenhängende Platte, an der sich kaudal die Anlage des Atlas anschliesst. Die Platte zeigt Rinnenform, indem ihre Seitenteile dorsalwärts gebogen sind. In der Rinne liegt die Chorda, die kaudalwärts die Anlage des Atlas durchbohrt. An der Blastemplatte finden sich ventral zwei wenig tiefe Einziehungen der Oberfläche (Fig. 2). Sie deuten in der Seitenrekonstruktion eine Aufteilung der Platte in drei Teile an. Der hinteren dieser Einziehungen gegenüber fehlt für eine kurze Strecke die dorsalwärts aufgebogene Kante der Blastemplatte. Hierdurch wird der kaudale Teil letzterer von dem grösseren, vorderen Rest abgesetzt und stellt die Anlage des s. g. Occipitalwirbels (FRORIEP 1886) dar. An dem übrigen Teil des Blastems wird eine Aufteilung durch die vordere Einziehung der ventralen Oberfläche angedeutet, und auch die Schnittbilder lassen undeutlich das Vorhandensein von zwei Blastemen hier erkennen. In dem folgenden Stadium (3,6 mm Kopflänge) hat sich das Blastem des Occipitalwirbels von dem vorderen Teil der ursprünglichen Blastemplatte ganz abgetrennt (Fig. 3). Gleichzeitig haben die dorsal gerichteten Seitenteile letzterer, die

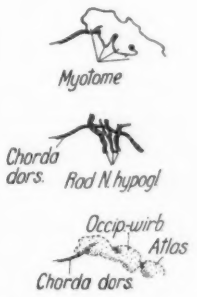

Fig. 2. Stad. I. Myotome, austretende Nerven und Skelettblasteme der Occipitalregion. Projektion von der Seite. 10/1.

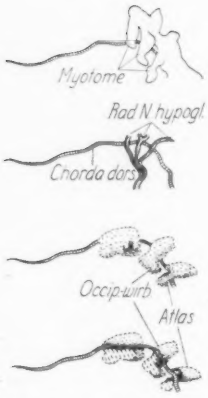

Fig. 3. Stad. II. Myotome, austretende Nerven und Skelettblasteme der Occipitalregion. Projektion von der Seite. 10/1.

Fig. 4. Stad. III. Myotome, austretende Nerven und Skelettblasteme der Occipitalregion. Projektion von der Seite. 10/1.

mehr oder weniger verschmolzenen Neuralbogen entsprechen dürften, stark an Grösse zugenommen. Auch hier können immer noch Andeutungen einer Segmentierung der vorderen Blastemmasse beobachtet werden. Die beiden getrennten Blasteme — besonders das des Occipitalwirbels — nehmen in der fortgesetzten Entwicklung stark an Grösse zu, nähern sich hierdurch einander und verschmelzen allmählich wieder in ihren basalen Teilen (Fig. 4). Die Seitenteile des Occipitalwirbels haben sich als typische Neuralbogen entwickelt und zeigen Fortsätze, die einer Prae- und einer Postzygapophyse entsprechen dürften. Eine Praezygapophyse findet sich auch an der Atlasanlage. Die Seitenteile des vor dem Occipitalwirbel liegenden Blastemabschnittes sind viel weniger entwickelt. Da die Chorda immer noch in einer dorsal offenen Rinne liegt, fehlen in der Occipitalregion Anlagen, die den Wirbelkörpern entsprechen.

In sämtlichen drei Stadien verläuft der erste Spinalnerv, d. h. der dem Occipitalwirbel zugehörige Nerv, zwischen den Anlagen dieses Wirbels und dem Atlas. Von den drei an Grösse von hinten nach vorn abnehmenden Wurzeln des N. hypoglossus zieht die 3. der vorderen Kante des Occipitalwirbels entlang, also kaudal von der vorderen Blastemmasse, während die 1. und 2. Wurzel lateral von dem hintersten Teil dieser Blastemmasse verläuft. Die Hypoglossuswurzeln sind in dem Stadium von 2,7 mm Kopflänge am längsten und werden in den zwei folgenden Stadien immer kürzer, d. h. das Zusammenschliessen der Wurzel zu dem Nerven erfolgt in dem erstgenannten Stadium mehr ventral, um dann in den späteren Stadien immer weiter dorsal stattzufinden. Die 2. Wurzel ist in dem Stadium von 2,7 mm Kopflänge bis etwas ventralwärts von der Chorda gespalten. In dem Stadium 3,6 mm Kopflänge, haben sich die beiden Schenkel bis dorsal von der Chorda zusammengeschlossen. Schliesslich ist diese Wurzel in Stadium 4.4 mm Kopflänge so einheitlich wie die anderen zwei.

Jeder der drei Hypoglossuswurzeln sowie dem 1. Spinalnerven entspricht ein Myotom, das sich kaudolateral von dem zugehörigen Nerven befindet.

Die obenstehende Darstellung lässt in dem s. g. Occipitalwirbel einen verhältnismässig vollständig angelegten Wirbel erkennen. Das kranial davon gelegene, in gewissen Stadien ganz selbständige Blastem, das Anzeichen einer Metamerie zeigt, dürfte den zugehörigen Nerven und Myotomen nach weiteren

drei Wirbel entsprechen. Wie schon FRORIEP (1886) bei Bos feststellte, nehmen also an dem Aufbau der Occipitalregion auch bei Procavia vier Wirbelequivalente teil.

STADIUM IV: SCHEITEL-STEISS-LÄNGE 10 MM, KOPFLÄNGE 5 MM, FIG. 5.

Unter den schwer abzugrenzenden mesenchymatischen Verdichtungen dieses Stadiums fällt im hinteren Teil des Kopfes eine langgestreckte subcerebrale Platte, die Anlage der Basalplatte, auf. Sie ist hinten breit, hat die Form einer weiten Rinne und ist durch eine mediane, an einigen Stellen überbrückte Spalte in zwei laterale Hälften aufgeteilt. In der Rinne verläuft die Chorda von lockerem Bindegewebe umgeben. Der vordere Teil der Blastemplatte ist schmal und eben, und eine mediane Spalte in ihrer hinteren Hälfte fehlt. An der Stelle, wo der breite Abschnitt in den schmalen übergeht, dringt die Chorda in das Blastem ein, in dem sie bis halbwegs zu der Hypophyse verläuft und von dort weiter zwischen zwei Mesenchymverdichtungen bis kurz hinter den Hypophysenstiel. Unmittelbar hinter der Stelle, wo die Chorda in das Blastem eindringt, hat ein ganz kleines Gebiet des Blastems sich in vorknorpeliges Gewebe umgewandelt.

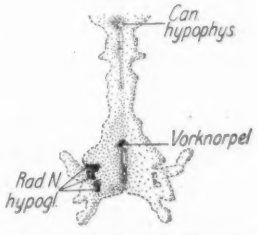

Fig. 5. Stad. IV. Projektion des Planum basale von dorsal. 10/1.

Der hintere breitere Teil der Blastemplatte zeigt Andeutungen einer Metamerie, die auf dreierlei Weise zum Ausdruck kommt: 1) Sein dorsalwärts gebogener Seitenteil ist durch drei medial gerichtete Einschnitte in vier Fortsätze aufgeteilt. Von diesen ist der 2. laterorostral und der 3. und 4. nach laterokaudal gerichtet, während der kurze, breite 1. Fortsatz sich seitlich streckt. 2) Die drei Wurzeln des Nervus hypoglossus treten durch das Blastem an drei Stellen, die in rostrokaudaler Richtung nacheinander liegen, die vordere durch den besonders tiefen Einschnitt zwischen Fortsatz 1 und 2, die zwei folgenden durch „Foramina", die in einigem Abstand von dem Rand liegen. Im Verhältnis zu den beiden hinteren Einschnitten sind die zwei Foramina, besonders das hintere, nach vorn verschoben. 3) Die mediane Spalte wird von verdichtetem Mesenchym an drei Stellen überbrückt, die auf der Höhe des medialen Endes des vordersten Einschnittes und der zwei Foramina ausgebildet sind. — Der hinterste Fortsatz dürfte auf Grund seiner Beziehung zu der 3. Wurzel des N. hypoglossus als Neuralbogen des Occipitalwirbels anzusprechen sein, während die drei vorderen eventuell demselben Element drei weiterer Wirbel entsprechen (vgl. oben). — Auch an zwei anderen, etwas weiter entwickelten Exemplaren ist die Basalplatte untersucht worden. Hier sind nur drei Fortsätze vorhanden. Die zwei Durchgangsstellen der hinteren Hypoglossuswurzel sind rostrad ge-

rückt. Das verknorpelte Gebiet hat zugenommen und streckt sich in dem einen Embryo nach hinten halbwegs bis zu dem hinteren Rand der Basalplatte. In dem anderen hat es sich etwas nach vorn, aber hauptsächlich nach hinten und lateral ausgebreitet.

Mesenchymatische Verdichtungen finden sich weiter an gewissen Teilen der Ohrenkapsel, rings um den Hypophysenstiel, in der künftigen Lamina trabecularis und dem Septum nasi. Unmittelbar hinter dem Hypophysenstiel ist das Blastem unpaarig im Gegensatz zu dem der vorderen Basalplatte.

DIE ENTWICKLUNG DES GESAMTEN CHONDROKRANIUMS.

STADIUM V: SCHEITEL-STEISS-LÄNGE 12 MM, KOPFLÄNGE 6 MM, FIG. 6—10.

Eine markierte Abknickung der sonst geraden Schädelbasis ist wie in dem Stadium von 10 mm auf der Grenze zwischen der Basalplatte und der Hypophysenplatte vorhanden. Die als knorpelig angegebenen Teile bestehen aus sehr jungem Knorpelgewebe.

Die Verknorpelung des Planum basale ist weit fortgeschritten. Der stabförmige vordere Teil von diesem ist verknorpelt bis auf die Höhe des einheitlichen Foramen acusticum. Der breite, hintere Teil, der immer noch die Form einer offenen Rinne hat, ist kaudal paarig infolge einer engen von dem hinteren Rand rostralwärts einschneidenden Spalte. Auch ein Stück weiter nach vorn kommt das paarweise Auftreten der Verknorpelungszentren in der Struktur zum Ausdruck. In dem hinteren Teil der Basalplatte streckt sich das Knorpelgewebe lateralwärts bis zu dem einheitlichen Foramen hypoglossi, kaudalwärts an dem rostrolateralen Rand des künftigen Foramen magnum entlang bis in die Pila occipitalis. Diese besteht aus zwei Schenkeln, von denen der hintere dorsalwärts aufgerichtete sich als Blastem fortsetzt und den zwei hinteren Fortsätzen des vorigen Stadiums entspricht, der vordere, ganz aus Blastem bestehende lateral von dem Foramen hypoglossi ausgeht und sich nach vorn umbiegt. Dieser Schenkel entspricht wenigstens in seinem basalen Teil den zwei hinteren Fortsätzen des vorigen Stadiums. Das einzige Foramen hypoglossi dürfte seiner Lage nach etwa der Durchtrittstelle der vordersten Hypoglossuswurzel entsprechen. Beiderseits der Incisura intercondyloidea buchtet sich ein kleines Blastem hervor, das an der ventralen Fläche mit dem des vorderen Schenkels der Pila occipitalis verbunden ist. Die Chorda dorsalis verläuft hier wie im Stadium I dorsal von dem hinteren, breiten Teil der Basalplatte, um dann in diese einzudringen (Fig. 7, 9). Das häutige Labyrinth ist immer noch wenig weit differenziert. So haben Utriculus und Sacculus eine breite Verbindung miteinander, der Ductus cochlearis ist kurz und zeigt noch keine Aufrollung, und der horizontale Bogengang hat immer noch im Gegensatz zu den beiden vertikalen Bogengängen die Form einer langgestreckten Tasche, die

sich gröstenteils dem Planum basale parallel streckt. Das häutige Labyrinth ist von einem Blastem eingehüllt, das dorsal in dem Gebiete der künftigen Prominentia cruris communis und des anschliessenden Teils der Prominentia semicircularis posterior sehr dünn ist. Dieses Gebiet dünnen Blastems streckt sich sowohl an der medialen wie an der lateralen Fläche der Kapsel ventralwärts hinunter und enthält die Durchtrittsöffnung des langen Ductus endolym-

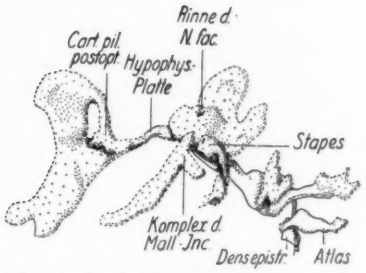

Fig. 6. Stad. V. Projektion von der Seite. 10/1.

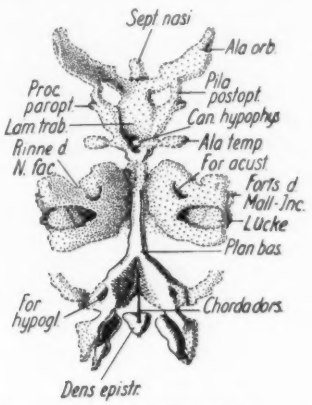

Fig. 7. Stad. V. Projektion von dorsal. 10/1.

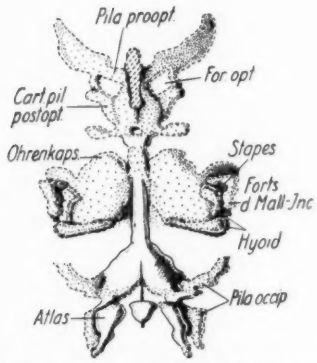

Fig. 8. Stad. V. Projektion von ventral. Rostraler Teil des Septum nasi abgeschnitten. 10/1.

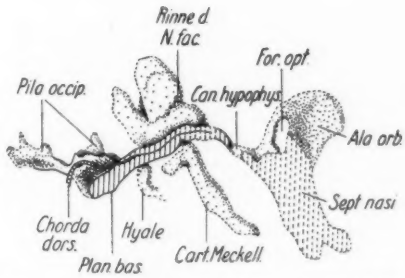

Fig. 9. Stad. V. Projektion von medialer Sektion. 10/1.

phaticus. Sonst ist das Ohrenkapselblastem auffallend dicht in dem ventrolateralen Teil der Pars canalicularis. Die Lagebeziehungen von Pars cochlearis und Pars canalicularis sind dieselben wie in dem definitiven Chondrocranium, d. h. Pars canalicularis liegt in der Hauptsache dorsal und etwas kaudal von der Pars cochlearis. Auf der Grenze dieser beiden Teile findet sich an dem vorderen Rand der blastematischen Kapsel ein Einschnitt, durch den der

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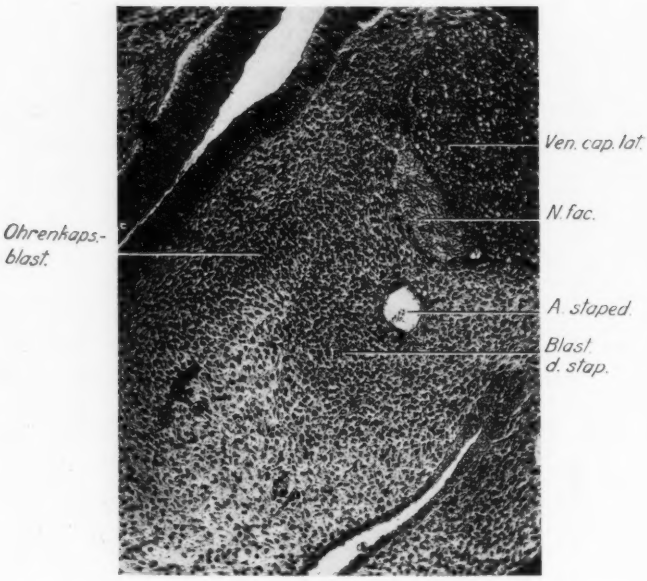

Fig. 10. Stad. V. Schnitt durch das Blastem des Stapes. 100/1.

Nervus facialis zieht. Die Anlage der eigentlichen Schneckenkapsel ist stark seitlich geneigt. In der Transversalebene bildet ihre grösste Ausdehnung einen Winkel von 65° mit der Medianebene. Im mittleren Teil der Ohrenkapsel verhält sich die Pars vestibularis in derselben Weise wie eben für die Schneckenkapsel angegeben, die Pars canalicularis richtet sich dagegen auf, sodass die grösste Ausdehnung in der Transversalebene einen Winkel von 30° mit der Medianebene bildet. Die Kapsel ist also hier mediodorsalwärts konkav. Im hintersten Teil beträgt derselbe Winkel etwa 45°. An der lateralen Fläche der blastematischen Ohrenkapsel zieht schon als langgestreckte Erhebung die Prominentia semicircularis lateralis der Basalplatte etwa parallel. Ventral von dieser Erhebung findet sich in einer seichten Eindellung in dem Blastem die sehr weite Vena capitis lateralis, die von vorn nach hinten über die Oberfläche der Ohrenkapsel zieht. Rostral von dem vordersten blastematischen Teil des Planum basale findet sich in der sonst unverknorpelten Lamina trabecularis ein quergestelltes Knorpelstück, das sich nach vorn bis zu dem Processus alaris streckt und nach DE BEER (1937) als Hypophysenplatte zu bezeichnen ist. In Form von Blastem befinden sich ferner die verhältnismässig sehr breite Pars chiasmatica, das Septum nasi, der mittlere Teil der Ala orbitalis mit den Pilae prooptica und postoptica, die Cartilago pilae postopticae und der kaudal von dem Nervus maxillaris liegende Teil der Lamina ascendens alae temporalis, der in den blastematischen Processus alaris übergeht.

Die Teile des Visceralskelettes, die unterschieden werden können, bestehen

aus verdichtetem Bindegewebe. Der Meckelsche Knorpel mit dem Malleus und die Incus bilden eine Einheit. Diese gibt dorsalwärts einen sich verjüngenden Fortsatz ab, der wahrscheinlich dem Crus breve incudis entspricht. Ein zweiter Fortsatz, der fast senkrecht auf dem Meckelschen Knorpel kaudalwärts gerichtet steht, dürfte die Anlage des Manubrium mallei und des Crus longum incudis ausmachen. Der mittlere Teil des Hyale kann als dichtes Blastem unterschieden werden. Dasselbe gilt für den von der Arteria stapedialis durchbohrten Stapes, der sich medioventral von der Vena capitis lateralis findet. Zwischen beiden zieht das Gewebe des Hyale als feiner Strang. Es soll besonders betont werden, dass das Stapesblastem, obwohl es dem Blastem der Ohrenkapsel dicht anliegt, von dem letzteren unterschieden werden kann (Fig. 10).

STADIUM VI: SCHEITEL-STEISS-LÄNGE 12 MM, KOPFLÄNGE 6,5 MM.

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Dieses Stadium, das dieselbe Scheitel-Steiss-Länge wie das zuletzt beschriebene, aber eine grössere Kopflänge aufweist und weiter differenziert ist, lag bereits als Schnittserie mit einer für graphische Rekonstruktion wenig geeigneten Schnittrichtung vor und wurde deswegen nicht vollständig rekonstruiert. Die Hauptbiegung der Schädelbasis liegt in der Hypophysenplatte. Die Verknorpelung hat so weit um sich gegriffen, dass sowohl das Foramen hypoglossi wie der Canalis hypophyseos von Knorpel umgeben ist. Die Wurzeln des Nervus hypoglossus verhalten sich an den beiden Seiten verschieden. An der einen treten sie, durch dicke bindegewebige Scheidewände voneinander getrennt, in den Knorpel ein. Hier verschwindet das trennende Bindegewebe zunächst zwischen zwei der Wurzeln, die sich zusammenschliessen, dann zwischen diesen zwei und der dritten, sodass sie alle drei dicht zusammen die äussere Mündung des Canalis hypoglossus verlassen. An der anderen Seite laufen bereits zwei der Wurzeln zusammen in den Knorpel ein, von der dritten durch eine bindegewebige Lamelle getrennt. Diese ist in dem weiteren Verlauf des Kanals sogar vorknorpelig, verschwindet aber gegen die äussere Mündung des Hypoglossus-Kanals, sodass die drei Wurzeln auch hier dicht zusammen diese verlassen. Der vordere Schenkel der Pila occipitalis hat sich verbreitert und sich sowohl dem hinteren Rand der Ohrenkapsel wie dem vorderen des hinteren Occipitalschenkels angeschlossen. Er bildet somit die Anlage der Lamina alaris Pilae occipitalis. Ventral fehlt die Verbindung zwischen dieser und der genannten Kapsel. Die Cartilago pilae postopticae, die hinsichtlich der Ausbildung der Knorpelstruktur verhältnismässig fortgeschritten ist, hat sich von dem angrenzenden Blastem gut abgesetzt. Es liegt hier ein selbständiges Verknorpelungszentrum vor. Neu entstandene Blasteme sind in der Nasenregion vorhanden. Lateral von dem Septum nasi und rostral von der blastematischen Pila prooptica findet sich eine mesenchymatische Verdichtung die sich mit dem dorsalen Septumrande verbindet. Sie stellt die Anlage der Cupula

posterior nasi dar. Lateral von dem vordersten Teil des Septum ist dorsal die erste Anlage des Paries als kleine, leicht gebogene Blastemplatte vorhanden. Auch das Solum ist in dem Gebiet der Lamina transversalis anterior als eine flügelartig von dem ventralen Rand des Septums lateral abstehende Blastemplatte angelegt. Das Visceralskelett verhält sich weitgehend übereinstimmend mit dem des zuletzt beschriebenen Stadiums. Es unterscheidet sich vor allem dadurch, dass es sich im allgemeinen viel einfacher abgrenzen lässt. So kann das Blastem des Hyale ohne Schwierigkeit verfolgt werden bis zu seinem kaudalen Ende, wo es einen dorsomedialen und einen dorsokaudalen Fortsatz abgibt. Ersterer bildet die von der Arteria stapedialis durchbohrte Anlage des Stapes und stösst nach vorn gegen den mächtigen kaudalwärts gerichteten Fortsatz des Malleus-Incus-Komplexes, ohne dass hier eine Grenze festgestellt werden kann. Der kleine, stumpfe, dorsolateral gerichtete Fortsatz stellt das künftige Laterohyale dar, das als Teil des Stylohyale verknorpelt.

STADIUM VII: SCHEITEL-STEISS-LÄNGE 15,5 MM, KOPFLÄNGE 7 MM, FIG. 11—13.

Die Biegung der Schädelbasis liegt teils in dem unverknorpelten Teil des Planum basale, teils — und zwar die Hauptbiegung — in der Hypophysenplatte.

Der vorderste Teil der Basalplatte ist immer noch unverknorpelt. Im hinteren schliesst sich die Rinne über dem vordersten Stück der freien Chorda. Die Stelle, an der diese in die Basalplatte eindringt, wird also nach hinten verschoben. Die äussere Mündung des Canalis hypoglossus ist einheitlich. An beiden Seiten treten aber die drei Hypoglossuswurzeln in die innere Mündung in zwei Gruppen ein, und diese verlaufen ein Stück in dem Kanal von einer dicken, unverknorpelten Bindegewebsschicht getrennt. Die beiden Schenkel der Pila occipitalis strecken sich in Form von Blastem weit dorsalwärts. Die Linie, entlang der sie sich gegenseitig berühren, tritt als weit offene Rinne hervor, da sie miteinander einen Winkel bilden. Bis auf ihre kurzen, dorsalen Spitzen, die durch einen wenig tiefen Einschnitt getrennt sind, haben sich die beiden blastematischen Schenkel der Pila occipitalis vollständig zusammengeschlossen. Von dem hinteren hängt in der Abb. 11 ein spitzer Zipfel kaudalwärts herunter. Dieser

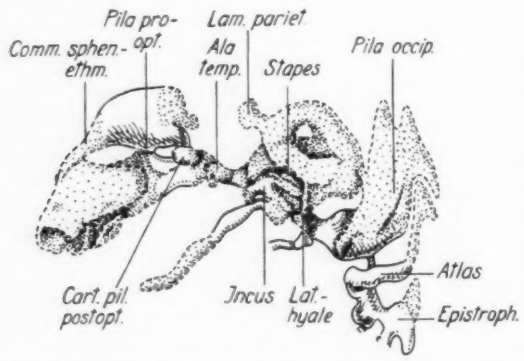

Fig. 11. Stad. VII. Projektion von der Seite. 10/1.

erscheint auch in dem Stadium von 16,5 mm und dürfte die Folge einer bei der Präparation durch Schrumpfung und Verbiegung entstandenen Inkongruenz zwischen dem abgezeichneten und bei der Rekonstruktion verwendeten und dem beim Schneiden tatsächlich vorliegenden Profil zurückzuführen sein. Der vordere Schenkel verbindet sich an seiner rostralen Kante auf einer kurzen Strecke mit dem Ohrenkapselblastem. Obwohl das betreffende Stadium durchgehend viel weiter entwickelt ist als das Stadium III, zeigt dieses eine viel breitere Verbindung zwischen Pila occipitalis und Ohrenkapsel. Ventral findet sich zwischen beiden eine grosse Öffnung, durch die die Nervi glossopharyngeus und vagus und Vena jugularis passieren, und von dessen lateraler Begrenzung das Blastem des Processus paracondyloideus nach ventral ausgeht. Aus dem Blastem der Ohrenkapsel hat sich der erste Knorpel auf der medianen Fläche ventral von dem einheitlichen Foramen acusticum entwickelt. Im übrigen zeigt das Ohrenkapselblastem eine grosse, durchgehende Öffnung an dem Ort der Fossa subarcuata anterior einen nach vorn gerichteten Fortsatz, die Anlage der Lamina parietalis und der Commissura parietocapsularis und eine hohe, mit dem Planum basale parallel verlaufende Crista parotica. Über seiner rostralen Kante zieht der Nervus facialis immer noch in einer offenen Rinne, und an seiner ventralwärts gekehrten Fläche öffnet sich das Foramen perilymphaticum. Die knorpelige Hypophysenplatte ist immer noch nur durch Blastem mit dem vorderen Teil der Basalplatte, der Pars chiasmatica der Lamina trabecularis und der Cartilago pilae postopticae verbunden. Ihre laterale Verknorpelung ist weiter fortgeschritten, sodass knorpelige Processus alares vorhanden sind. Die Ala temporalis besteht immer noch ganz aus Blastem. Dieses entspricht der Spina alaris, dem kaudal von dem Foramen rotundum befintlichen Teil der Lamina ascendens und dem an diese beiden anschliessenden Abschnitt der Lamina pterygoidea, die aber sehr kurz ist, und verbindet sich mit dem Processus alaris. Eine kleine, wenn auch nicht sehr starke mesenchymatische Verdichtung findet sich auch vor dem Foramen ovale. Soweit die Anlage der Ala temporalis ausgebildet ist, zeigt sie dieselben Beziehungen zu dem Nervus maxillaris, dem Nervus vidianus und der Arteria maxillaris interna wie in dem fertigen Chondrokranium. Zu bemerken ist, dass der Nervus mandibularis hier im Gegensatz zu den endgültigen Verhältnissen durch eine Einbuchtung in das Blastem passiert, die der Incisura ovalis entspricht. Dies hängt mit der hier vorliegenden rostralen Lage des Ganglion semilunare zusammen, das sich rostralwärts bis auf die Höhe des vorderen Randes des Foramen rotundum erstreckt. Verknorpelt ist weiter der ventrale vordere Teil der Lamina trabecularis und das mittlere Gebiet der Ala orbitalis mit der Pila postoptica und die Wurzel der Pila prooptica. Von der Wurzel der letztgenannten breitet sich eine Knorpelplatte in dem dorsalen Teil der Lamina trabecularis aus. Diese Platte ist zum Teil durch Blastem von der ventralen Verknorpelung getrennt. Quer über die Pila prooptica läuft aber eine

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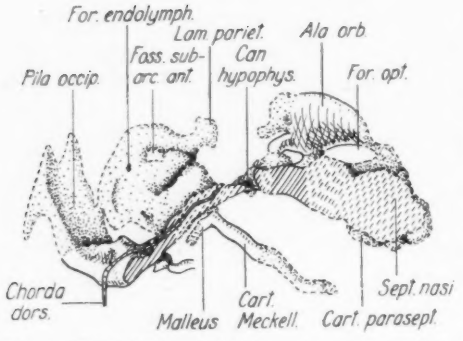

Fig. 12. Stad. VII. Projektion von medianer Sektion. 10/1.

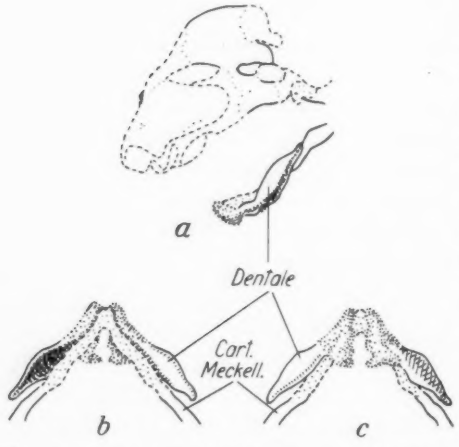

Fig. 13. Stad. VII. Deckknochen. *a* Vorderer Teil des Schädels in Projektion von der Seite; *b* und *c* Unterkiefer in Projektion von dorsal resp. von ventral. 10/1.

schmale Zone aus Blastem, die zeigt, dass die Ala orbitalis und die Pilae proopticae getrennt verknorpelt werden. Eine selbstständige Verknorpelung liegt also in der Ala orbitalis vor. Diese ist hinter der Pila postoptica wie auch vorn, wo sie sich über die blastematische Commissura sphenoethmoidalis mit dem Paries nasi verbindet, als Blastem angelegt. Das ganze Septum nasi besteht immer noch aus verdichtetem Bindegewebe wie der vorderste, kurze Teil der Lamina trabecularis. Die ganze Nasenseitenwand liegt als Blastem vor, und die Verlängerung der Nasenkapsel rostral von dem Septum ist auch vorhanden. Sowohl die Lamina transversalis posterior wie der Paraseptalknorpel sind blastematisch angelegt. Durch ihre Grösse fällt die Cartilago pilae postopticae auf, die sich eben in einem Zwischenstadium zwischen Blastem und Vorknorpel befindet. Das hier vorliegende selbstständige Verknorpelungszentrum setzt sich schon durch die Ausbildung eines Perichondriums von umgebendem Blastem ab. — Die hintere Hälfte der Cartilago Meckeli wie das Capitulum mallei ist verknorpelt. Von diesem setzt sich das Manubrium mallei als sehr dicker und dichter blastematischer Fortsatz kaudalwärts fort. Auch das Corpus incudis ist bis auf seinen vordersten Teil verknorpelt, der zwar einen knorpeligen Kern enthält, im übrigen aber aus Blastem besteht und dem Capitulum mallei aufliegt. Die beiden Crura incudis sind sehr lang und schlank und in ihren basalen Teilen auch verknorpelt. Crus breve streckt sich der Crista parotica entlang und krümmt sich hierbei etwas dorsalwärts. Crus longum steht in Beziehung zu dem Stapes aber auch zu dem Hyale, wie wir bald sehen werden und streckt sich auch nach hinten. Das Hyale besteht aus zwei sich verschieden verhaltenden Teilen, die von einer dünnen Schicht aus Perichondrium getrennt wer-

den. Diese Schicht entspricht dem Ligament der verknorpelten Hyalspange. Das Blastem des „Epihyale" ist weit entwickelt und steht eben vor der Verknorpelung. Dasselbe gilt für den Teil des dorsalen Abschnittes des Hyale, der an das Epihyale grenzt, während in den übrigen Teilen eine histologische Differenzierung noch nicht eingesetzt hat. Die blastematische Spange passiert rostral von dem Nervus facialis, und die Chorda tympani tritt an ihrer lateralen Seite aus. Sie zweigt ein kurzes, stumpfes, laterodorsal gerichtetes Laterohyale ab und zieht medialwärts, wo sie in das Blastem des Stapes und in das hintere Ende des Crus longum incudis übergeht. Das Blastem desjenigen Teiles der Crista parotica, mit dem sich das Stylohyale später verbindet, ist immer noch sehr wenig verdichtet.

Als erster Deckknochen erscheint hier das Dentale lateral von dem mittleren Teil des Meckelschen Knorpels.

In einem anderen Embryo (Körperlänge 15 mm, Kopflänge 7,5 mm), der etwas weiter entwickelt ist, finden sich ausser dem Verknorpelungszentrum ventral von dem einheitlichen Foramen acusticum noch einige Gebiete mit beginnender Verknorpelung in dem Ohrenkapselblastem und zwar an seiner lateralen Fläche ein kleines Gebiet von der Crista parotica und eine kleine Fläche dorsal von dem vorderen Teil der Fossa subarcuata.

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STADIUM VIII: SCHEITEL-STEISS-LÄNGE 16,5 MM, KOPFLÄNGE 8 MM, FIG. 14—17.

Die Hauptbiegung liegt auf der Höhe des hinteren Teiles der Cartilago pilae postopticae. Im Verhältnis zu dem zuletzt beschriebenen Stadium sind folgende Veränderungen eingetreten. Von der Gegend des Processus paracondyloideus ist eine blastematische Brücke rostrodorsalwärts gewachsen und hat sich mit dem ventrokaudalen Teil des Ohrenkapselblastem vereinigt. Hierdurch ist zum Teil die ventrale und laterale Begrenzung des Recessus jugularis entstanden. Zwischen dieser Brücke und der schon vorher vorhandenen ist eine Lücke in dem Blastem zurückgeblieben. Das verdichtete Bindegewebe der Pila occipitalis hat sich dorsalwärts stark ausgedehnt und in dieser Richtung eine grosse, dünne Lamelle gebildet, die Anlage der Cartilago supraoccipitalis. Zwischen dieser und dem Blastem der Lamina parietalis ist auch der übrige Teil der Lamina supracapsularis angelegt worden. Von dem Ohrenkapselblastem ist zwischen dem vorderen Ende der Crista parotica und der Commissura parietocapsularis als stumpfer, rostroventral gerichteter Fortsatz die Anlage des Tegmen tympani ausgewachsen. Hier ist auch eine blastematische Commissura suprafacialis entstanden. Die Basalplatte, die in ihrer ganzen Ausdehnung fast dieselbe Höhe zeigt, ist vollständig verknorpelt und verbindet sich homokontinuierlich mit der Hypophysenplatte. Die die Chorda dorsalis enthaltende Rinne der cerebralen Fläche hat sich noch weiter nach hinten geschlossen. Der freie Teil der

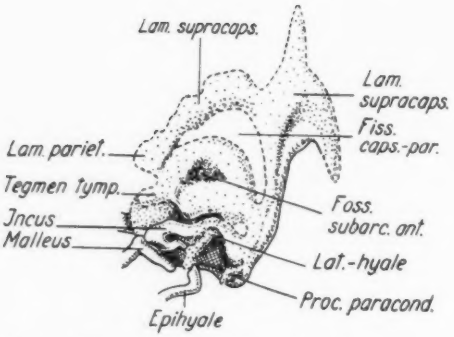

Fig. 14. Stad. VIII. Otical- und Occipitalregion. Projektion von der Seite. 10/1.

Chorda ist folglich ganz kurz geworden; der in dem Knorpel verlaufende ist immer noch in seiner ganzen Ausdehnung erhalten und streckt sich bis auf die Höhe der vorderen Kuppel der Ohrenkapsel. Die Verknorpelung der Pila occipitalis hat sich längs derem hinteren Rand dorsalwärts weit ausgedehnt. Die Wurzeln des Nervus hypoglossus ziehen beiderseits in zwei von einer bindegewebigen Lamelle getrennten Gruppen durch den ganzen Canalis hypoglossus und vereinigen sich erst nach dem Austreten aus diesem zu einem Stamme. An der medialen Fläche der Ohrenkapsel sind zwei weitere Verknorpelungszentren hinzugekommen, das eine zwischen der kleiner gewordenen Fossa subarcuata anterior und dem einheitlichen Foramen acusticum und das andere kaudal von diesem Zentrum und ventral von dem Foramen endolymphaticum, sodass hier deren drei vorhanden sind. An der lateralen Fläche besteht ein Gebiet längs der Crista parotica aus Knorpel, das sich bis zu dem vordersten Teil der Prominentia semicircularis anterior ausdehnt. Der umgebogene Teil von diesem wird ganz von Knorpel gebildet. Hier steht folglich Knorpel der lateralen und der medialen Fläche der Ohrenkapsel miteinander in Verbindung. In der Ala temporalis hat die Verknorpelung eingesetzt und zwar in einem Gebiet kaudal von dem Foramen rotundum und lateral von dem Processus alaris. Von diesem wird der Knorpel der Ala temporalis immer noch durch Blastem getrennt. Die Cartilago pilae postopticae ist verknorpelt, wird aber sowohl von der Lamina trabecularis wie von der Pila postoptica durch ein Perichondrium getrennt. Sonst besteht im vorderen Teil des Schädels weitgehende Übereinstimmung mit den Verhältnissen des Stadium IV. Hervorzuheben ist, dass die Cupula posterior nasi wie in den folgenden Stadien sich im Verhältnis zu der Pila prooptica weiter nach hinten streckt als in dem ausgebildeten Chondrochranium. Der hintere Teil des Septum nasi ist vorknorpelig und scheint ein selbständiges Verknorpelungszentrum zu repräsentieren. — Der Meckelsche Knorpel mit dem Malleus ist mit Ausnahme der Spitze des

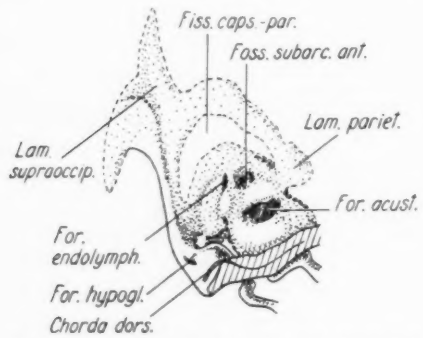

Fig. 15. Stad. VIII. Otical- und Occipitalregion. Projektion von medianer Sektion. 10/1.

Fig. 16. Stad. VIII. Fossa hypophyseos mit Alae temporales. Projektion von dorsal. 10/1.

Manubrium mallei verknorpelt. Die Verknorpelung der Incus ist weiter fortgeschritten, doch bestehen der hintere Teil des Crus breve und der Endteil des Crus longum, der sich hier nicht nur nach hinten, sondern auch nach medial streckt, aus Blastem. Dieses lässt sich für das kaudale Ende des ersteren nicht scharf gegen das Blastem der Ohrenkapsel abgrenzen. Auch in dem Stapes ist ein knorpeliger Kern vorhanden, der hauptsächlich in den Crura stapedis liegt und von hier aus ein kleines Stück in die künftige Fussplatte eindringt. Dieser Knorpelkern lässt sich in dem ausgebildeten Chondrokranium immer noch von dem später aufgelagerten Knorpel gut unterscheiden. Das Blastem der Fussplatte grenzt sich von dem Ohrenkapselblastem ab, und auch zwischen dem Crus longum incudis und dem Stapes besteht kein Zusammenhang mehr. Die Hyalspange

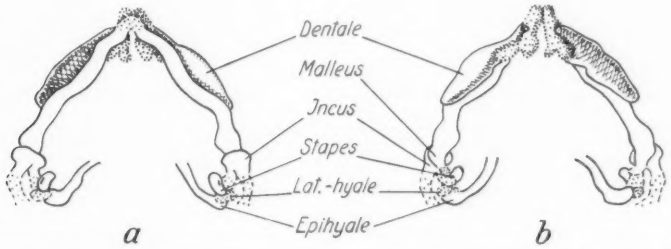

Fig. 17. Stad. VIII. Deckknochen. Unterkiefer sowie dorsales Ende des Meckelschen Knorpels und des Hyoidbogens. *a* Projektion von dorsal; *b* von ventral. 10/1.

ist bis auf kleine Reste verknorpelt. Von dem Stylohyale liegt sowohl die Ventralspange wie Verbindungsspange als Knorpel vor. Nur die Querspange befindet sich eben in dem Übergang zwischen Blastem und Vorknorpel. Der mediale Schenkel des Hyale geht etwa von der Verbindungsspange des Stylohyale aus und ist mediorostral gerichtet. Er legt sich von ventral an das Crus longum incudis und den Stapes an, wo sich diese gegenseitig berühren, ist aber von beiden abgesetzt.

STADIUM IX: SCHEITEL-STEISS-LÄNGE 18 MM, KOPFLÄNGE 9 MM.

Dieses Exemplar lag als ältere Schnittserie vor, mit einer Schnittrichtung, die eine vollständige graphische Rekonstruktion unmöglich macht. Ich beschränke mich deswegen darauf, nur mit einigen Angaben Lücken zwischen V und VII möglichst auszufüllen.

Eine hohe, knorpelige Lamina supracapsularis biegt sich über die Ohren-

kapsel und geht hinten in die Cartilago supraoccipitalis über, an der ein Tectum posterius fehlt. Zwischen dem knorpeligen Teil der Pila occipitalis und dem der Lamina supraoccipitalis liegt ein breites Gebiet von Blastem. Die Verknorpelung letzterer ist also nicht von der Pila occipitalis ausgegangen. Ob sie im Zusammenhang mit diesem Vorgang in der Lamina parietalis stattgefunden hat, lässt sich nicht entscheiden. Auch die Commissura parietocapsularis ist wie der mit ihr verbundene Teil der Ohrenkapsel verknorpelt. — An dem Teil des Septum nasi, der sich durch die vordere Hälfte des Foramen olfactorium streckt, besteht der dorsale Teil immer noch aus Blastem. Sonst ist das Septum verknorpelt, der vorderste Teil allerdings aus sehr jungem Knorpel bestehend. In der Pars praecerebralis ist das Tectum hinter dem Foramen epiphaniale, und zwar von dem dorsalen Septumrand aus als Cartilago paratectalis teilweise verknorpelt. Rostral von dem genannten Foramen ist das Tectum blastematisch. Gegen den lateralen Rand des verknorpelten Tectum stösst unter Verwachsung eine knorpelige Platte (Cartilago paranasalis) des Paries nasi. Als Rest dieser Verwachsung bleibt kaudal die sich zwischen der Incisura praecribrosa und dem Foramen epiphaniale streckende Grenzfurche zurück. Weiter nach vorn, wo die Verknorpelung noch nicht eingesetzt hat, grenzt sich das Blastem entlang derselben Linie in zwei Platten ab, die sich mit ihren Kanten berühren. Der Verwachsungslinie entlang zieht der Ramus lateralis des Nervus ethmoidalis, und an der auf der Innenseite leicht hervorstehenden Kante der Seitenwand entwickelt sich das Blastem des Nasoturbinale. Die Knorpelplatte der Cartilago paranasalis hört hinten auf der Höhe der vorderen Ecke des Foramen olfactorium auf und streckt sich nach vorn mit abnehmender Breite bis zu der Höhe des vorderen Endes des Paraseptalknorpels.

STADIUM X: SCHEITEL-STEISS-LÄNGE 19 MM, KOPFLÄNGE 10 MM, FIG. 18—25.

Bis auf kleinere Bezirke, besonders in der Regio otica, liegt die Anlage des ganzen Schädels jetzt vor. Von allgemeinen Zügen möchte ich folgendes hervorheben. Von der sehr hohen Cartilago supraoccipitalis geht das schmale kaudodorsal gerichtete Tectum posterius und in entgegengesetzter Richtung die hier gerade verlaufende Lamina supracapsularis aus. Diese hört nach vorn mit einer auffallend grossen Lamina parietalis auf, die sich nach vorn über den vorderen Pol der Schneckenkapsel streckt und dem hinteren Ende der Ala orbitalis ziemlich nahe kommt. Da die Ohrenkapsel im Verhältnis zu dem von der Lamina supracapsularis, der Cartilago supraoccipitalis und der Pila occipitalis gebildeten Bogen immer noch klein und stark zur Seite geneigt ist, stellt die Fissura capsuloparietalis eine grosse Öffnung dar. Die Commissura basicapsularis wird erst in diesem Stadium als Blastem angelegt. Im vorderen Teil

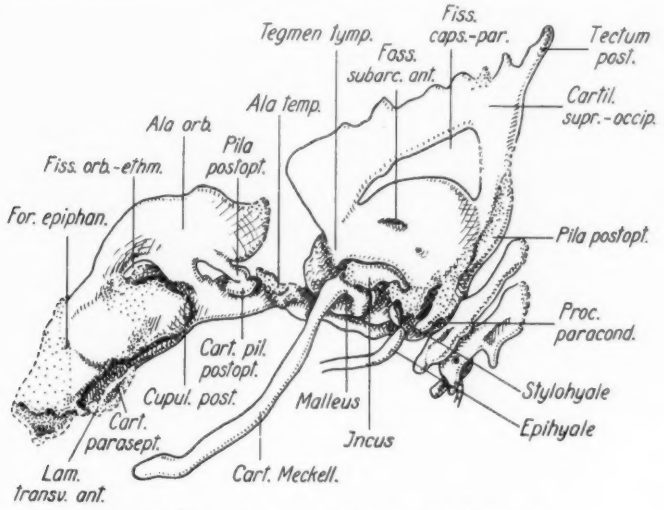

Fig. 18. Stad. X. Projektion von der Seite. 10/1.

des Kopfes fällt die Cartilago pilae postopticae immer noch durch ihre Grösse auf. Die Ala orbitalis hat sich seitlich niedergelegt. Bemerkenswert ist, dass die Cupula posterior nasi sich bis hinter das hintere Ende der Fissura orbitonasalis erstreckt. Das sowohl absolut wie relativ hohe Septum zeigt grösste Höhe an der Grenze zwischen Pars subcerebralis und Pars praecerebralis in etwa

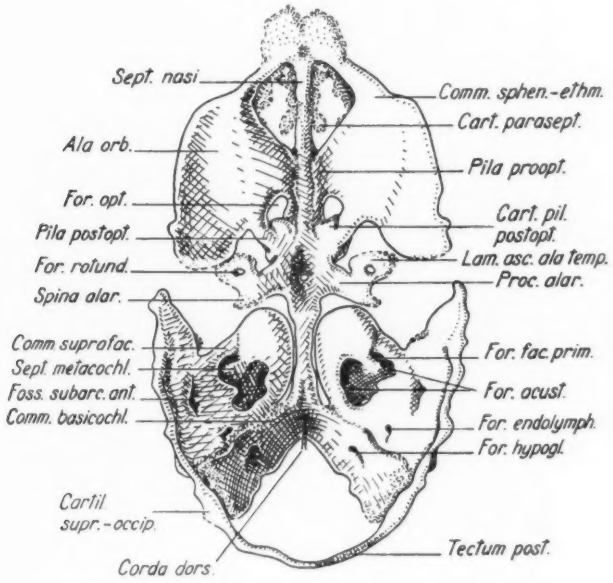

Fig. 19. Stad. X. Projektion von dorsal. 10/1.

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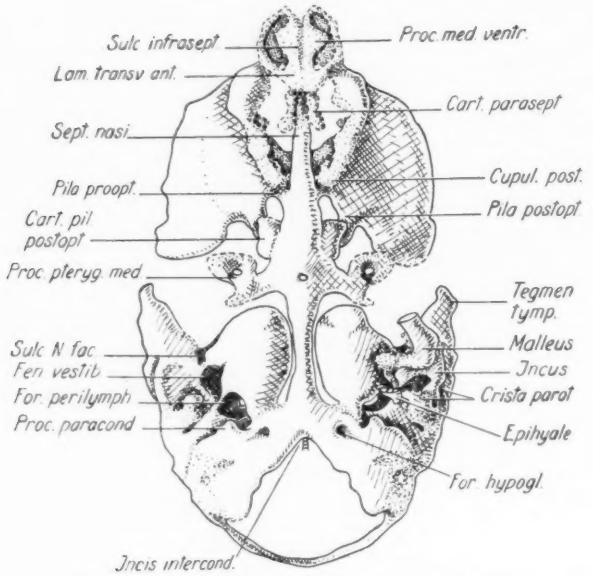

Fig. 20. Stad. X. Projektion von ventral. 10/1.

gleichem Abstand von dem vorderen und dem hinteren Ende der Nasenkapsel. Diese macht etwa ein Drittel der Gesamtlänge des Schädels aus. Die Hauptbiegung der Schädelbasis liegt auf der Höhe der Pila prooptica.

Die Basalplatte hat angefangen dicker zu werden, besonders in ihrem vorderen Teil und die die Chorda enthaltende Rinne hat sich weiter nach hinten geschlossen (vgl. Fig. 21). Der in dem Knorpel eingeschlossene Teil der

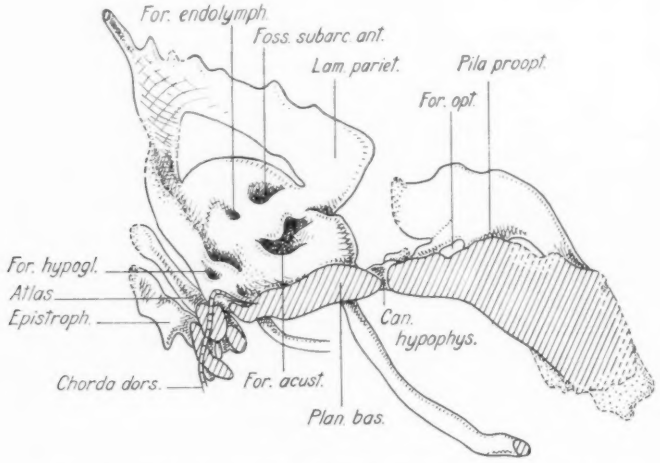

Fig. 21. Stad. X. Projektion von medialer Sektion. 10/1.

Chorda ist bis auf einen kleinen hinteren Rest verschwunden. Die drei Hypoglossuswurzeln laufen dicht zusammen durch das an beiden Seiten einfache Foramen hypoglossum. An der Pila occipitalis ist ventral die rostrale Kante der Lamina alaris blastematisch und schliesst sich teilweise noch nicht vollkommen an den hinteren Rand der Ohrenkapsel an. An der Pila occipitalis ist die Rinne immer noch sehr auffallend, deren Seiten die beiden blastematischen Schenkel der jüngeren Stadien ausmachen, und an der entlang eine schmale Zone noch unverknorpelt ist. Die sich von dorsal zwischen dieser Zone und der Ohrenkapsel einschiebende Knorpellamelle, die sich mit der letzteren homo-

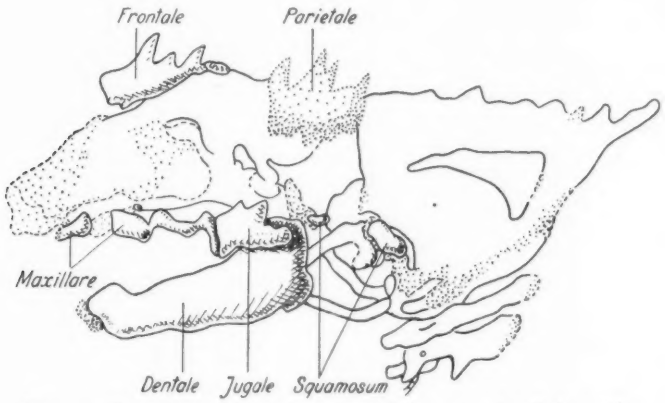

Fig. 22. Stad. X. Deckknochen. Projektion von der Seite. 10/1.

kontinuierlich verbindet, ist wahrscheinlich von der Cartilago supraoccipitalis aus verknorpelt. Ihre Verbindung mit der letztgenannten ist nämlich als wohl entwickelter Knorpel aufgebaut, während die Verbindung mit der Ohrenkapsel aus ganz jungem Knorpel besteht. An der lateralen Fläche dieser Kapsel liegt die vordere Spitze des Tegmen tympani und das kaudale Gebiet des ventral von der Fossa incudis sich streckenden Teiles der Crista parotica als Blastem vor. Das hintere, ebenfalls aus Blastem aufgebaute Ende des Crus breve incudis geht ohne Grenze in dieses Blastem der Crista parotica über, das sich nach hinten als ventralwärts herabhängende, kurze Lamelle entlang der Prominentia semicircularis lateralis fortsetzt und kaudal von dem ventralen Teil der Lamina alaris durch eine lange Spalte getrennt wird. Auch rings um die Fussplatte des Stapes ist die Ohrenkapselwand blastematisch. Die mediale Fläche der Kapsel ist ganz verknorpelt, das Septum metacochleare als Blastem vorhanden. Von der Ala temporalis sind der laterale Teil der Lamina ascendens, der kaudale Teil der Spina alaris und die Spitzen der beiden kurzen Processus pterygoidei nur verknorpelt. Die Knorpelplatte der Ala temporalis ist schon homokontinuierlich mit dem Processus alaris verbunden. Dagegen besteht noch ein grosser Zwischenraum zwischen seinem vorderen Rand und der Cartilago

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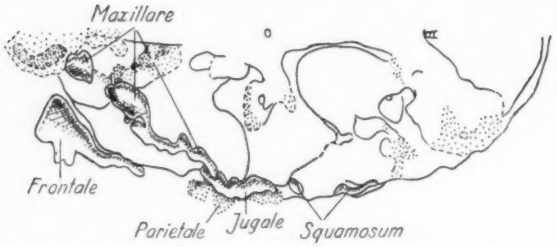

Fig. 23. Stad. X. Deckknochen. Projection von ventral. 10/1.

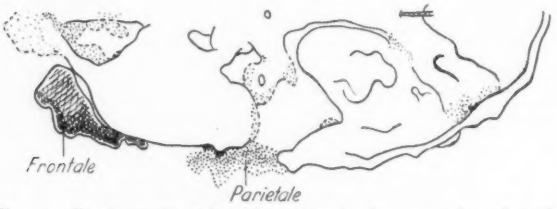

Fig. 24. Stad. X. Deckknochen. Projection von dorsal. 10/1.

pilae postopticae. Letztere ist hier homokontinuierlich verbunden, sowohl mit der dorsolateralen Kante der Lamina trabecularis, von der sie lateralwärts absteht, wie mit der Pila postoptica. Bis auf ein kleines Stück der kaudalen Ecke der Ala orbitalis ist letztere vollständig verknorpelt. Die sehr breite Pila prooptica geht hinten auf einer kleinen Strecke laterodorsal —, sonst lateralwärts von der Lamina trabecularis ab. In der Nasenregion ist die Verknorpelung am wenigsten fortgeschritten. In dem vorliegenden Exemplar besteht der dorsale Septumrand in der hinteren Hälfte der Pars subcerebralis aus Blastem. Sonst ist das Septum bis auf eine ziemlich breite, dorsorostrale Kante unverknorpelt. In dem Tectum der Pars praecerebralis befindet sich die schon beschriebene quergestellte Knorpelplatte, die aber hier an der Oberfläche paarig erscheint und sich zum Teil durch Blastem von der Verknorpelung des Paries abgrenzt. In diesem sind zwei verschiedene Knorpelgebiete vorhanden, von denen das eine, Cartilago antorbilis, sich hinter dem Sulcus lateralis posterior ausbreitet, das andere, die Cartilago paranasalis, sich von dieser Furche nach vorn streckt bis zu einer Linie, die das Foramen epiphaniale mit dem vorderen Ende der Lamina transversalis posterior verbindet. Die Cartilago paranasalis stösst dorsal gegen und verbindet sich mit dem Parietotectalknorpel und dehnt sich ventral über den Sulcus lateralis anterior nach vorn aus. Das Maxilloturbinale liegt ausschliesslich als Blastem vor. Das Foramen epiphaniale befindet sich nicht wie in dem Stadium IX rostral von dem vorderen Ende des Foramen olfactorium, sondern lateroventral und etwas rostral. An dem Solum nasi ist die Lamina transversalis posterior in Form von Blastem vorhanden. Von der Cartilago paraseptalis findet sich

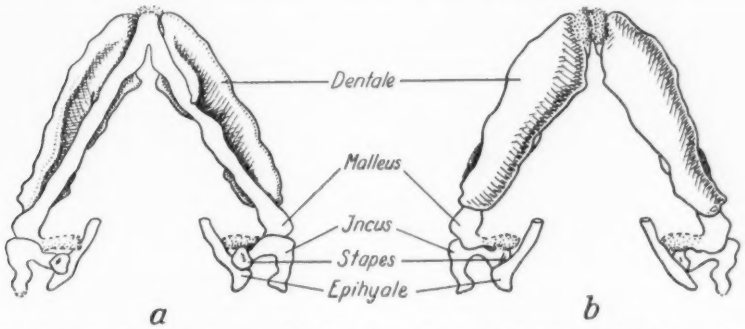

Fig. 25. Stad. X. Unterkiefer mit Meckelschem Knorpel, Gehörknöchelchen und Hyoid. *a* Projektion von dorsal; *b* von ventral. 10/1.

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nur die mediale Lamelle, die von dem Septum aus verknorpelt. Dies gilt auch für die Lamina transversalis anterior, deren blastematische Platte hinten lateral gerichtet ist und etwas dorsal von dem lateralen Rand des Septum ausgeht, sodass diese sich als kleiner knorpeliger Wulst unter die Platte senkt. Vorn geht das Blastem der Lamina transversalis anterior ventrolateral und zwar von dem Rand selbst ab, den Sulcus infraseptalis bildend, in dem die von dem Septum aus verknorpelnde Cartilago papillae palatinae den genannten Wulst ein kleines Stück nach vorn fortsetzt. — Der Meckelsche Knorpel ist bis auf den rostralen unpaarigen Fortsatz verknorpelt. An dem Visceralskelett ist sonst das Endstück des Manubrium mallei, der rostralste Teil des Corpus incudis, das Ende der beiden Crura incudis und der periphere und mediale Teil der Fussplatte des Stapes unverknorpelt. Die Arteria stapedialis ist immer noch kräftig.

Von Deckknochen liegen hier Dentale, Squamosum, Jugale, Maxillare und Frontale vor, während Parietale nur als Blastem vorhanden ist (Fig. 22—25).

STADIUM XI: SCHEITEL-STEISS-LÄNGE 22 MM, KOPFLÄNGE 11 MM, FIG. 26—33.

Die Hauptbiegung der Schädelbasis liegt hier auf der Höhe der Pila prooptica. Im Grossen und Ganzen hat sich der Schädel wenig im Vergleich zu Stadium X verändert. Die Verknorpelung ist weiter fortgeschritten, sodass sie in der Hauptsache — eine Ausnahme ist die Nasenregion — abgeschlossen ist. In der Basalplatte ist die Chorda dorsalis vollständig resorbiert. Die drei Hypoglossuswurzeln passieren auf der einen Seite durch einen einheitlichen Kanal hindurch, in dessen innerem Ende die eine Wurzel von den anderen zwei durch eine dicke, bindegewebige Scheidewand getrennt wird. An der anderen Seite hat der Hypoglossuskanal nach innen zwei Mündungen, nach aussen eine. Durch die hintere der erstgenannten treten eine, durch die vordere zwei durch

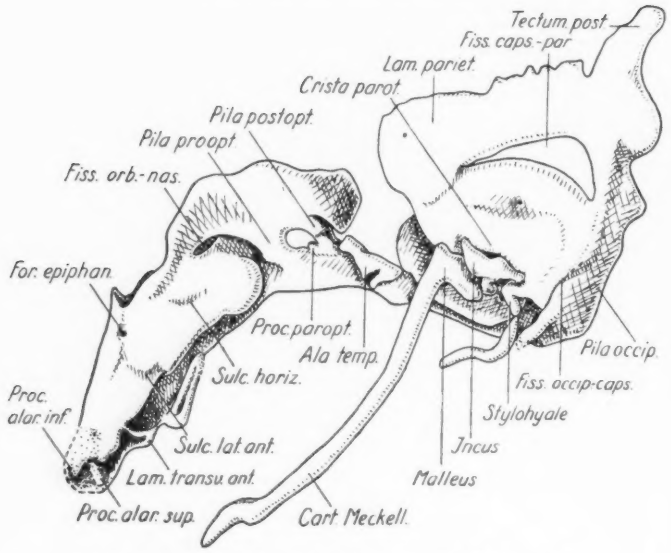

Fig. 26. Stad. XI. Projektion von der Seite. 10/1.

ein dickes Bindegewebe getrennte Wurzeln in den Kanal ein. Die Ohrenkapsel, deren Volumen sich zu dem der Schädelhöhle wie 1 : 38 verhält, lehnt sich immer noch, besonders in der Pars cochlearis, stark zur Seite. Ein Aufrichten der Kapsel findet also zwischen diesem und dem Stadium XII statt. In der Ohrenkapsel sind die nächste Umgebung der Fenestra vestibuli, ein Teil des Septum metacochleare und die das Foramen acusticum aufteilende Knorpelplatte immer noch unverknorpelt. Die Verbindung zwischen der vorderen Kante der Lamina alaris und der Ohrenkapsel ist nur dorsal verknorpelt und besteht weiter ventralwärts aus Blastem. Zum grossen Teil liegt aber hier eine dünne, durch Bindegewebe geschlossene Spalte vor, die als Fortsetzung des Foramen jugulare eine Fissura occipitocapsularis posterior darstellt, und die später durch Knorpel geschlossen wird. Die blastematische Lamelle des Stadium VII, die von dem ventralen Teil der Crista parotica kaudalwärts verläuft und sich hier entlang der genannten Fissur streckt, ist von der Crista parotica aus verknorpelt worden. Wo dieser Knorpel sich vorn mit der Prominentia semicircularis lateralis von ventral verbindet, legt sich die hintere Spitze des Crus breve incudis von der Seite der Ohrenkapselwand an. Weiter nach vorn ist das Crus breve zur Hälfte in die Fossa incudis eingesenkt, die eine ventralwärts offene Rinne bildet, und in der Tiefe der Fossa ist es mit der Kapselwand durch ein Blastem verbunden. Bis auf einen dünnen Streifen aus Blastem nahe an der Basalplatte ist die Commissura basicochlearis verknorpelt. Die Ala temporalis hat sich noch nicht mit der Cartilago Pilae postopticae verbunden, und an dem vorderen Rand der Lamina ascendens ist die Verknorpelung noch

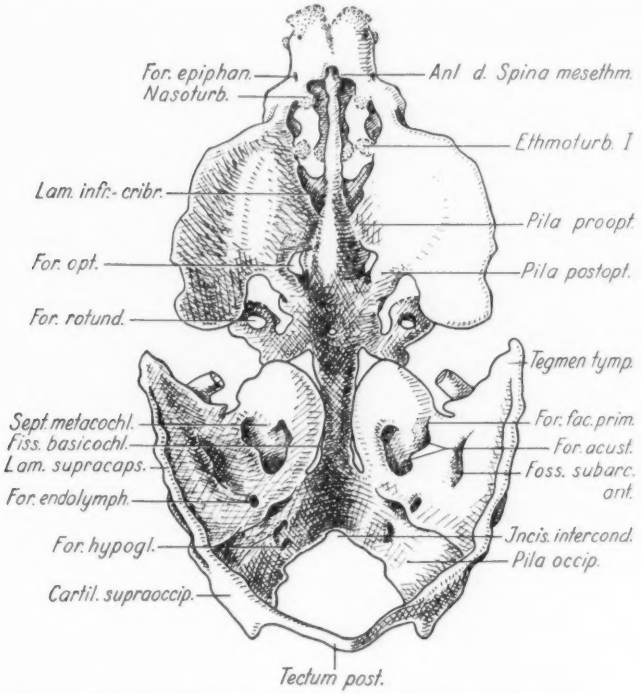

Fig. 27. Stad. XI. Projektion von dorsal. 10/1.

nicht abgeschlossen. Diese hat sich zusammen mit der Pila postoptica nach dorsal und medial aufgerichtet, sodass der Processus paropticus jetzt lateral von dem hinteren Teil des Foramen opticum zu liegen kommt. Eine ähnliche Aufrichtung hat die Pila prooptica erfahren, besonders in ihrem hinteren Teil. Dieser Vorgang setzt sich weiter fort (vgl. Stadium XII). Die Proportionen der Nasenkapsel, die hier wie in dem vollausgebildeten Chondrokranium zwei Fünftel der Gesamtlänge des Schädels ausmacht, haben sich verändert. Der subcerebrale Teil macht weniger als die Hälfte (4/9) der Kapsel aus. Besonders der vor der Lamina transversalis anterior liegende Teil hat sich verlängert und zwar besonders der röhrenförmige praeseptale Abschnitt der Nasenkapsel. Das Foramen epiphaniale liegt hier fast so weit dorsalwärts und nach vorn wie in Stadium XII. Die Crista mesethmoidalis wird durch paarige knorpelige Anlagen repräsentiert, die als mediodorsale Verlängerungen der Cristae praecribrosae erscheinen. Zwischen den beiden Fortsätzen passieren die zwei kleinen Arterien, die in dem vollgebildeten Chondrocranium das Septum in einer kleinen Grube rostral von der Spina ethmoidalis durchbohren. Das Septum nasi ist vollständig verknorpelt, der Paries nasi bis auf einen rostrodorsalen Rest, der auch auf die mediale Wand des praeseptalen Kapselabschnittes übergreift, sowie die Verbindung des Paries mit der Lamina trans-

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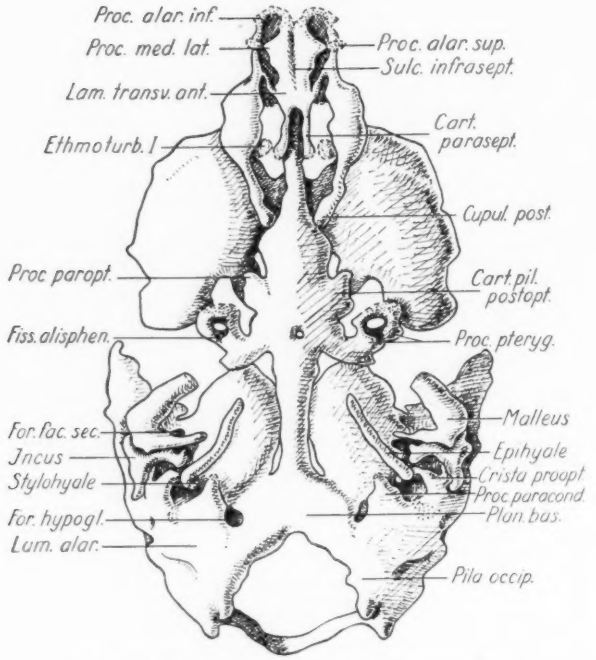

Fig. 28. Stad. XI. Projektion von ventral. 10/1.

versalis anterior. Von grossem Interesse ist, dass das Blastem hier dorsal von der Fenestra narina in einem Gebiet, das bei Equus, Bos u. a. von der Fenestra superior eingenommen wird, sehr stark verdünnt ist. Durch ein Loch, das in Fig. 26—27 zu sehen ist, tritt hier ein kleines Gefäss durch. Von dem ventralen

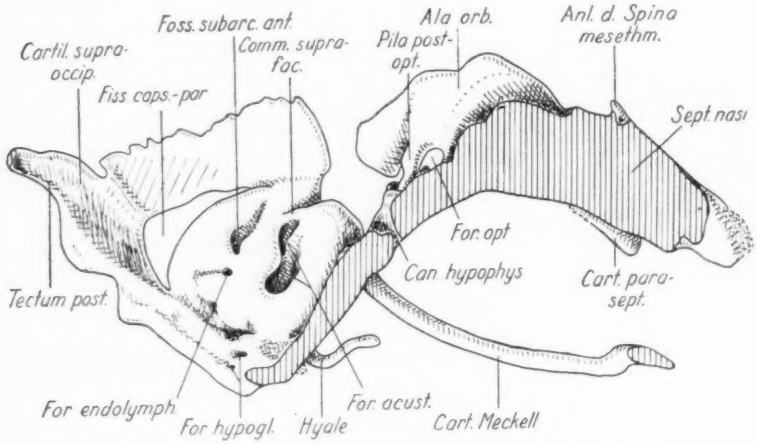

Fig. 29. Stad. XI. Projektion von medialer Sektion. 10/1.

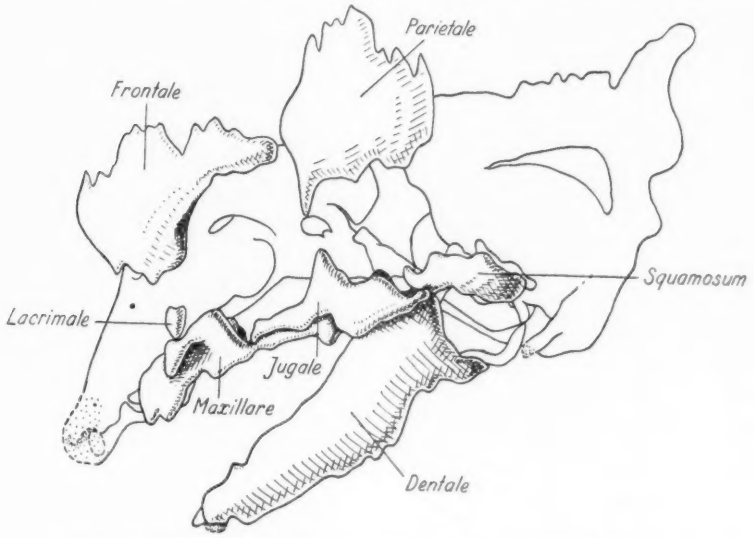

Fig. 30. Stad. XI. Deckknochen. Projektion von der Seite. 10/1.

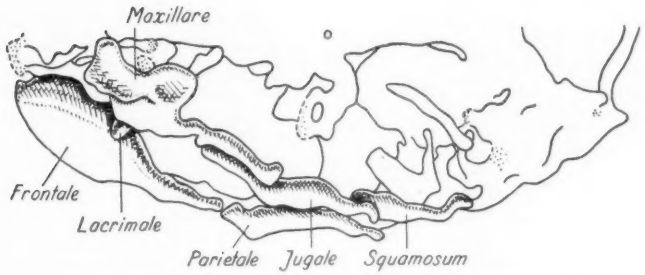

Fig. 31. Stad. XI. Deckknochen. Projection von ventral.

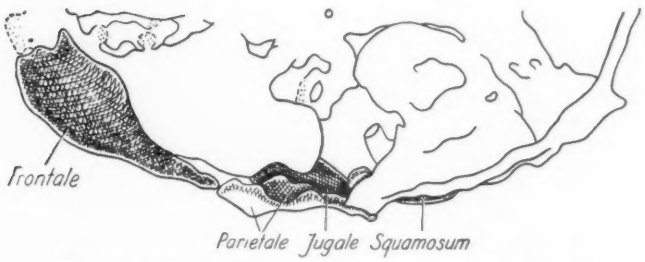

Fig. 32. Stad. XI. Deckknochen. Projection von dorsal.

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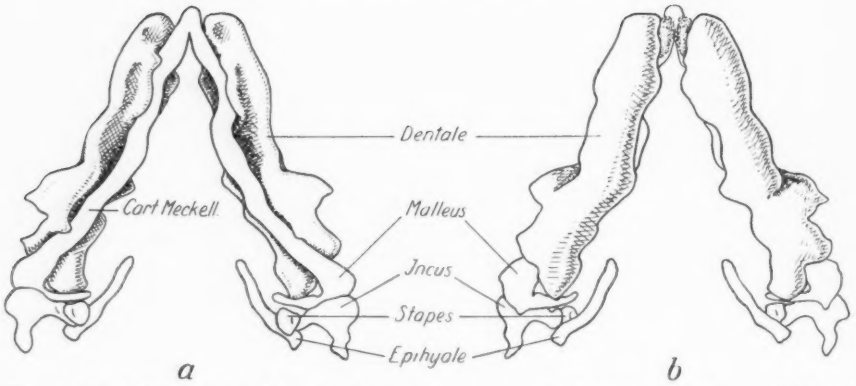

Fig. 33. Stad. XI. Unterkiefer mit Meckelschem Knorpel, Gehörknöchelchen und Hyoid. *a* Projektion von dorsal; *b* von ventral. 10/1.

knorpeligen Teil des praecerebralen Kapselabschnittes ist der Processus ventralis lateralis ausgebildet. Die beiden Processus alares bestehen dagegen aus ganz dünnem Blastem. Auch das Solum nasi ist weitgehend verknorpelt. Dies gilt der Lamina transversalis anterior wie, bis auf ihren medialen Rand, auch der Lamina transversalis posterior. Von dem Paraseptalknorpel ist die mediale Lamelle, die sich nur nahe dem Übergang in die Lamina transversalis anterior auf einer ganz kurzen Strecke mit dem Septum verbindet, verknorpelt. In dem hinteren Teil liegt die laterale Lamelle noch in Form von Blastem vor. Ethmoturbinale I und II, Maxilloturbinale und Nasothurbinale sind in blastematischer Form angelegt worden. Die drei erstgenannten entstehen im Anschluss an schon verknorpeltes Gewebe, während das letztgenannte sich selbstständig entwickelt und erst sekundär sich dem Knorpel anschliesst. — Das Visceralskelett ist bis auf den Stapes vollständig verknorpelt. In dem medialen und peripheren Teil der Fussplatte hat die Verknorpelung auf der Grenze zu dem zentralen Kern eingesetzt, ist aber von dieser nicht sehr weit fortgeschritten. Die Arteria stapedialis ist immer noch vorhanden, obwohl verhältnismässig klein.

Zu den schon in Stadium X vorhandenen Deckknochen Dentale, Squamosum, Jugale, Maxillare, und Frontale sind Parietale und Lacrimale hinzugekommen (Fig. 30—33).

DAS VOLL ENTWICKELTE CHONDROCRANIUM.

STADIUM XII: SCHEITEL-STEISS-LÄNGE 33 MM, KOPFLÄNGE 14 MM, FIG. 34—67.

a. Planum basale.

Das Planum basale, die Grundlage der Schädelbasis in der Regio occipitalis und der Regio otica, streckt sich als kräftiger Balken von dem

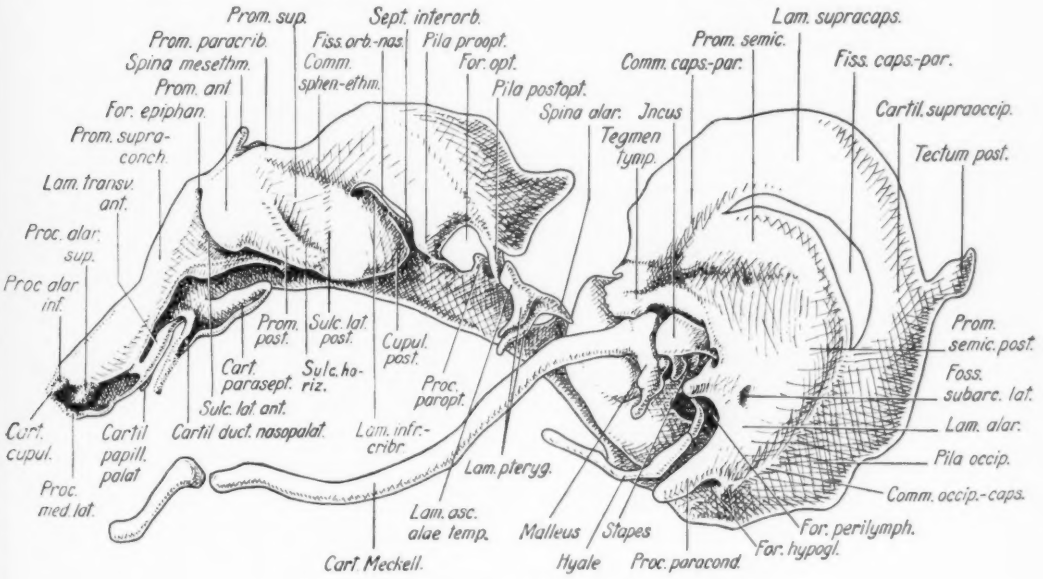

Fig. 34. Stad. XII. Projektion in der Seite. 10/1.

Foramen magnum bis zu der Fossa hypophyseos. Kaudal ist es breit und flach, wird nasalwärts schmäler und höher. Abgesehen von dem hintersten Siebentel des Balkens, der sich parallel zur Längsachse des Chondrocraniums ausdehnt, bildet die ventrale Fläche des Planum basale fast eine Gerade, die zu der obengenannten Achse in einem Winkel von etwa 45° steht (Fig. 37). Der Übergang zwischen der grösseren Breite des hinteren Abschnittes und der geringeren des vorderen geht nicht allmählich, sondern ziemlich unvermittelt vor sich (Fig. 35). Die Basalplatte gliedert sich hierdurch in zwei Abschnitte, deren Grenze jedoch nicht mit der kaum zu erkennenden zwischen Pars occipitalis und Pars otica plani basalis zusammenfällt, sondern weiter rostralwärts liegt.

Der kaudale Abschnitt des Planum basale ist eine verhältnismässig dünne Platte, die etwa ebenso lang wie breit ist. Seine hintere, gleichmässig breite Hälfte setzt sich seitlich in die Commissura basi-cochlearis fort, die vordere dagegen hat die Form eines Trapezes, dessen kürzeste (rostrale) Seite etwa halb so lang wie die gegenüberstehende ist. Die seitlichen, von der Fissura basi-cochlearis begrenzten Ränder des Trapezes verlaufen nicht gerade, sondern leicht nach aussen gebogen. Hinten ist das Planum basale durch die von dem Foramen magnum aus leicht einschneidende Fissura intercondyloidea in zwei kurze Schenkel gespalten (Fig. 35, 36), die kaudal unmittelbar in die Pilae occipitales übergehen. Die Foramina hypoglossi begrenzen lateral den kaudalsten Teil der Basalplatte. — Die dorsale Fläche des kaudalen Abschnittes der Basalplatte ist schwach konkav, die ventrale entsprechend schwach konvex

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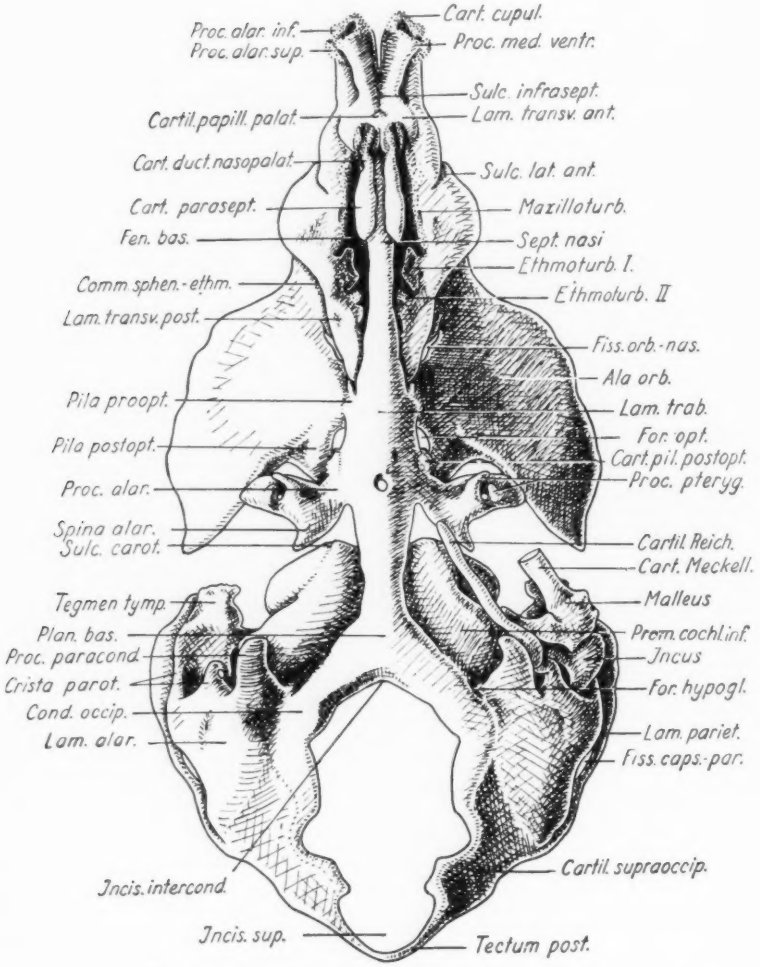

Fig. 35. Stad. XII. Projection von ventral. 10/1.

(Fig. 41, 42). Durch eine nur auf der dorsalen Fläche der Platte hervortretende Verdickung kommt hier ein niedriger Wulst zustande, der, senkrecht zur Längsrichtung des Planum basale verlaufend, die kaudalen Ränder der Fissurae basicochleares verbindet. Am dünnsten ist der betreffende Abschnitt der Basalplatte in der Mitte, rostral und kaudal von diesem Wulst. Sowohl gegen den freien hinteren Rand wie lateralwärts nimmt die Stärke der Knorpelplatte zu.

Eine kleine Abknickung an der ventralen Fläche des Schädelbodens unmittelbar kaudal von der Mündung des Canalis hypophyseos (Fig. 37) stellt den Ort der Verwachsung zwischen Paracordalplatte und Hypophysenknorpel dar

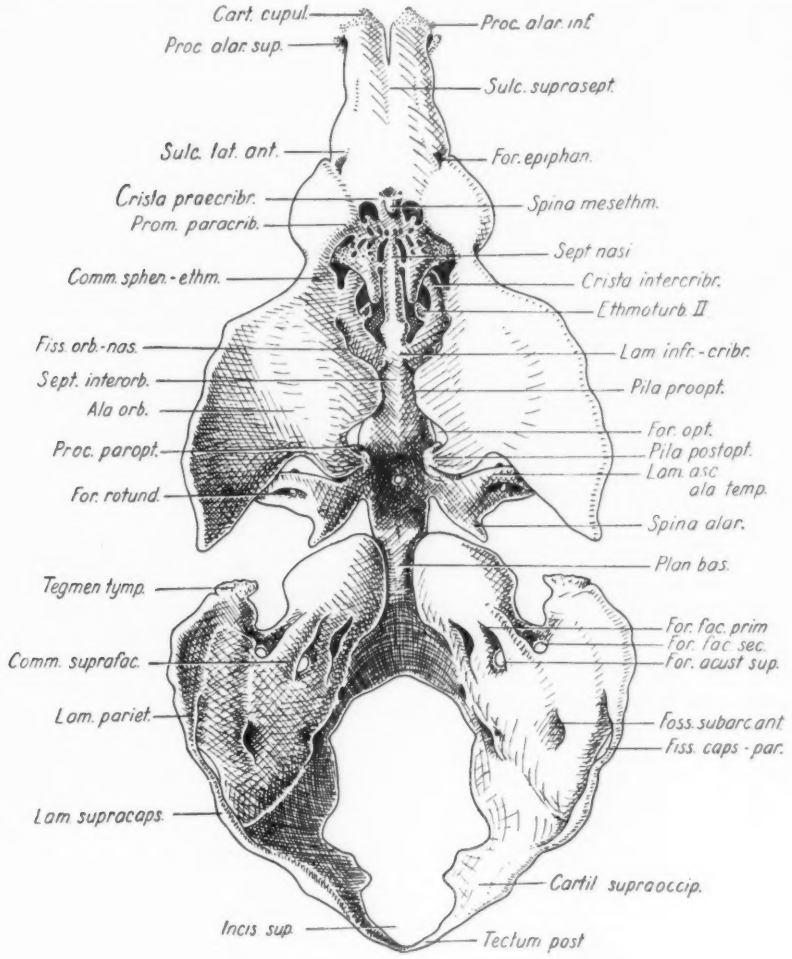

Fig. 36. Stad. XII. Projection von dorsal. 10/1.

(Fig. 37). Sonst geht der rostrale Abschnitt des Planum basale ohne Grenze in den Boden der Regio orbitotemporalis über. Dieser Abschnitt der Basalplatte hat die Form eines Stabes, der hinten, wo er in den kaudalen Abschnitt der Basalplatte übergeht, etwa doppelt so breit wie dick ist. Nach vorn nimmt er etwas an Breite ab, um bald wieder allmählich zuzunehmen und erreicht beim Übergang in die Regio orbitotemporalis fast die Breite seines kaudalen Endes (Fig. 35). Die schmalste Stelle findet sich etwa auf der Höhe der rostralen Spitze von Tegmen tympani. In seiner hinteren Hälfte nimmt der Knorpelstab rostralwärts nur unbedeutend an Höhe zu (Fig. 37), weiter nach vorn dagegen so beträchtlich, dass er hier höher als breit ist. Sowohl seine

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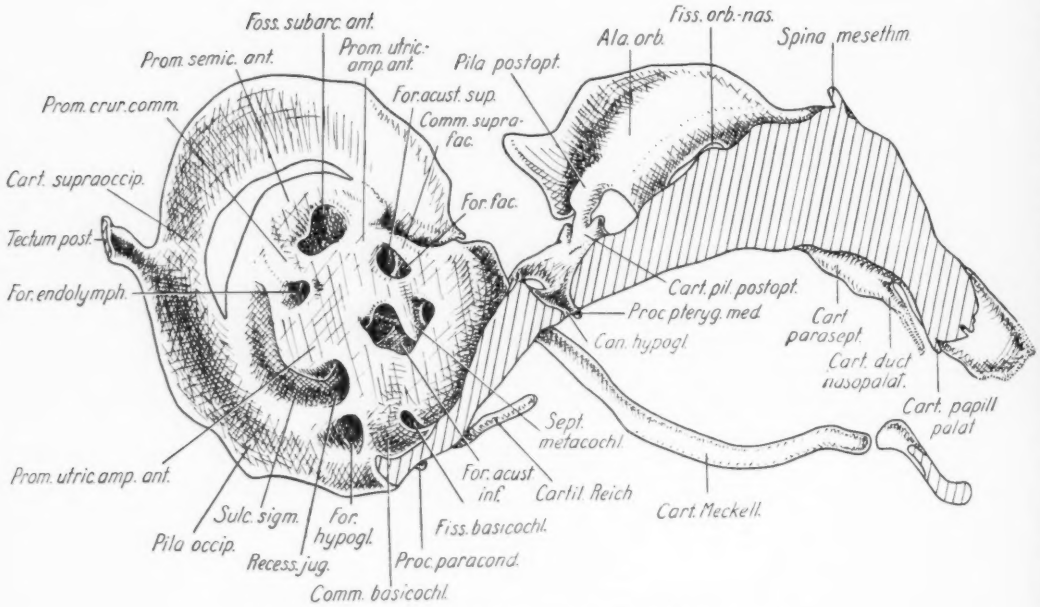

Fig. 37. Stad. XII. Projektion von medialer Sektion. 10/1.

ventrale wie seine cerebrale Oberfläche ist hier konvex (Fig. 45, 46). Letztere bildet auf der Grenze zu der Fossa hypophyseos zwei laterale, durch eine mediane Konkavität getrennte Höcker, die eine modifizierte Crista transversa darstellen (Fig. 36). Es fehlt jegliche Verbindung zwischen diesem Abschnitt des Planum basale und der Pars cochlearis, die durch die sehr lange Fissura basi-cochlearis getrennt werden. In dem Gebiet, in dem der kaudale, breite Teil in den vorderen, schmalen übergeht, kann der erste Anfang eines Abbaues des Knorpels beobachtet werden (Fig. 44 *).

Jegliche Spur einer Chorda dorsalis fehlt in dem vorliegenden Stadium.

b. Regio occipitalis.

Die Occipitalregion setzt sich aus der Pars occipitalis, Planum basale, den Pilae occipitales, den Cartilagines supra-occipitales und dem Tectum posterius zusammen. Charakteristisch für die Occipitalregion ist ihr enges Anschliessen an die Oticalregion.

Behalten wir den Namen Foramen occipitale magnum für die Öffnung, durch die die Medulla oblongata, vom spinalen Abschnitt des Nervus accessorius und von Blutgefässen begleitet, das Cavum cranii verlässt, so wird ein verhältnismässig grosser Teil, etwa ein Drittel, der weiten occipitalen Öffnung in diese Benennung nicht mit einbegriffen und als Incisura occipitalis superior bezeichnet. Fig. 38 stellt diese grosse Öffnung in einer

so gewählten Bildebene (von kaudoventralwärts gesehen) dar, dass die durch die Projektion entstehende Verkürzung für das Foramen magnum und für die Incisura occipitalis dieselbe ist. Wir finden also hier ein Foramen occipitale magnum, das etwa so hoch wie breit ist, mit der grössten Breite dorsal, wo es in zwei spitze Ecken ausläuft. Hiervon setzt sich die Incisura occipitalis superior durch eine deutliche Einengung der Öffnung ab.

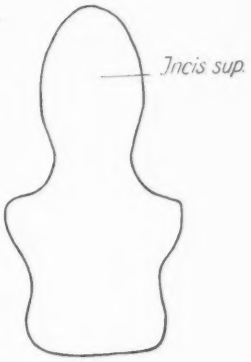

Fig. 38. Stad. XII. Begrenzungslinie des Foramen occipitale. Projektion von ventrokaudal. 10/1.

Das Foramen occipitale magnum liegt in einer Ebene, die einen Winkel von etwa 115° mit dem Planum basale bildet und nach ventral leicht konvex ist (Fig. 37). Seine lateralen Ränder werden von den Pilae occipitales gebildet, die sich ventral dem kaudalen Schenkel des Planum basale, dorsal den Commissurae basicochleares, anschliessen. Dieser ventrale Teil des Occipitalpfeilers streckt sich mit einer geringen lateralen Neigung in rostrokaudaler Richtung (Fig. 34, 37). Er zeigt demzufolge eine laterale und eine mediale Fläche und macht somit nicht Boden, sondern Seitenwand der Schädelhöhle aus (Fig. 39). Rostral, wo er an das Planum basale anschliesst, ist er sehr kräftig, nimmt aber kaudalwärts an Stärke ab und geht allmählich in eine dünne Knorpelplatte über.

Rostral an dem ventralen Rand der Occipitalpfeiler und lateral an dem kaudalen Schenkel des Planum basale sind die Condyli occipitales ausgebildet (Fig. 35). Sie sind paarige, langgestreckte, ventrolateral gerichtete, niedrige Höcker, deren Längsachsen nach rostral konvergieren und sich unter einem Winkel von 60—70° schneiden. Auffällig ist, dass die Berührungsfläche zwischen Condylus und Atlas vollkommen eben ist (Fig. 40). Während die benachbarten Teile der Occipitalpfeiler und der Basalplatte aus grosszelligem Knorpel bestehen, bauen sich die Occipitalcondylen aus kleinzelligem Knorpel auf. Eine Kommunikation zwischen den beiden Gelenkhöhlen besteht nicht.

Direkt dorsal von den Occipitalcondylen werden die Pilae occipitales eben auf der Grenze zu der Commissura basicochlearis und dem Planum basale von den aus einem Paar bestehenden, etwas ovalen, rostrolateralwärts blickenden Foramina hypoglossi durchbohrt. Der Nervus hypoglossus besteht aus drei Wurzeln, die nach aussen verfolgt sich zu einem Stamme vereinigen, nach innen sich weiter aufteilen. Ein dorsales Ganglion fehlt. Von dem grossen Raum des weiten Canalis hypoglossus nimmt der Nervus hypoglossus nur einen ganz kleinen Teil in Anspruch. Sonst wird der Kanal von der mit den vorderen Wirbelgeflechten in Verbindung stehenden „Rete canalis hypoglossi" ausgefüllt, das rechts aus mehreren kleinen, links aus einer grossen sinusähnlichen Vene besteht, die sich in die Vena jugularis interna dorsal von dem Processus paracondyloideus ergiesst.

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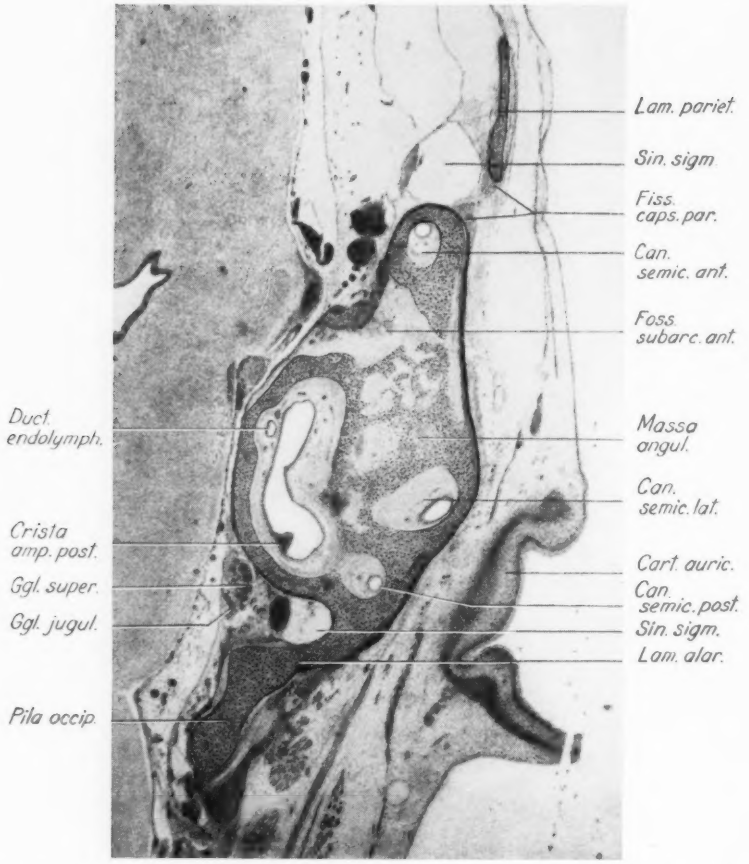

Fig. 39. Stad. XII. Schnitt durch den hinteren Teil der Pars canalicularis. 20/1.

Dorsal flachen sich die Pilae occipitales als Lamina alares ab (Fig. 34, 37, 39). Rostral bildet die Lamina alaris die ventrale und laterale Begrenzung des Foramen jugulare, das auf eine Linie mit dem Foramen hypoglossi und dem Condylus occipitalis fällt (Fig. 47), sowie den Boden und zum überwiegenden Teil die laterale Wand des Recessus jugularis (Fig. 39). Sie geht folglich hier lateralwärts als dünne Knorpellamelle ab, die mit einem runden Bogen nach dorsal umbiegt und sich in ihrer ganzen Länge homokontinuierlich mit dem ventro-lateralen Rand der Pars canalicularis der Ohrenkapsel verbindet, eine Commissura occipitocapsularis bildend. Dass hier eine Verlötung stattgefunden hat, kann immer noch an der Struktur des Knorpels erkannt werden. Die freie Kante der Lamina alaris setzt sich rostralwärts als Processus paracondyloideus fort (Fig. 34, 35, 47). Dieser stellt eine dreieckige, nach vorn etwas an Stärke zunehmende Platte dar, die

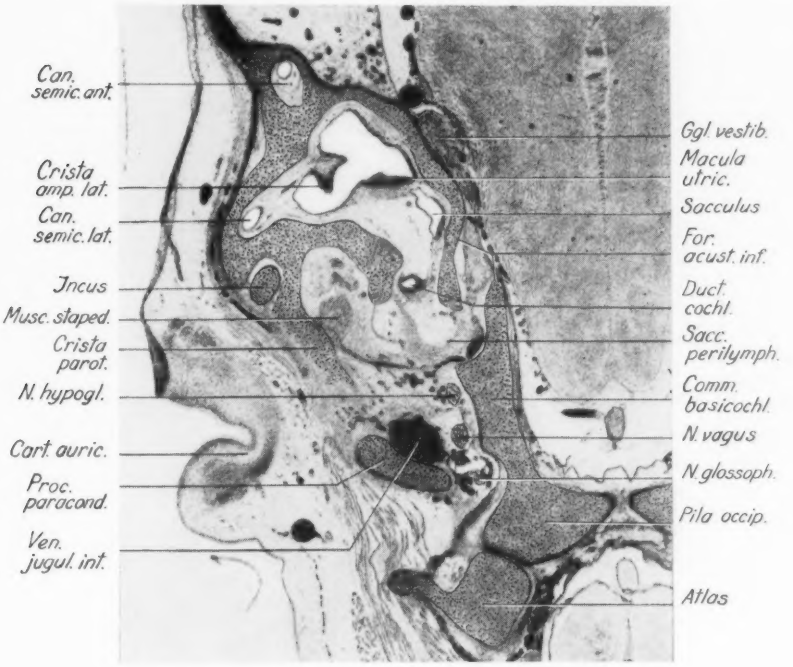

Fig. 40. Stad. XII. Schnitt durch Condylus occipitalis. 20/1.

stumpf endet (Fig. 40—42). Höhe und Basis sind in diesem Dreieck etwa gleich lang. — Recessus jugularis hat vorn in lateraler Richtung eine Ausdehnung, die anderthalb Mal der Höhe entspricht und grenzt sich hier durch gut abgesetzte Ränder von der eigentlichen Schädelhöhle ab. Weiter kaudalwärts wird die laterale Ausdehnung des Recessus jugularis kleiner und letzterer geht in den rinnenförmigen Sulcus sigmoideus über (Fig. 37), dessen Ränder abgerundet sind. Schliesslich erweitert sich der Sulcus hinten zu einer grossen, seichten und wenig abgegrenzten Konkavität, die sich sowohl über die Lamina alaris wie über den kaudalsten Teil der Pars canalicularis ausbreitet. Während die Lamina alaris rostral sowohl Boden wie laterale Wand des Recessus jugularis ausmacht, gehen in dem Sulcus sigmoideus diese beiden Teile ineinander über, indem die Lamina alaris dorsolateral abgeht und ohne grössere Biegung der Pars canalicularis zustrebt.

Die Pilae occipitales gehen kaudal und dorsal in die als dünne Knorpelplatten ausgebildeten Cartilagines supraoccipitales über (Fig. 34, 37). Weder kann die Verwachsungsstelle an der Struktur des Knorpels erkannt werden, noch machen Vergleiche mit jüngeren Stadien eine Festlegung der Grenze zwischen diesen beiden Elementen möglich. Allem Anschein nach bildet die Pila occipitalis auch einen grossen Teil des Randes der Incisura

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occipitalis, während sich die Cartilago supraoccipitalis rostral von diesem dorsalen Teil der Pila ventralwärts einschiebt. Die Cartilago supraoccipitalis ist medialwärts leicht konkav. Sie wird von der Pars canalicularis durch die Fissura capsuloparietalis getrennt und geht dorsal durch die breite Commissura occipitoparietalis, ohne dass hier eine Grenze angegeben werden kann, in die Lamina parietalis über (Fig. 34, 37).

Die beiden Cartilagines supraoccipitales sind durch ein dünnes, schmales Knorpelband, das Tectum posterius, miteinander verbunden (Fig. 34, 35, 37). Das Tectum hat eine rostrale und eine kaudale Fläche, die mit dem Planum basale einen Winkel von 45° bilden. Seine ventrale Kante macht die dorsale Begrenzung der Incisura occipitalis superior aus.

c. Regio otica.

1. *Als Ganzes.*

Die Regio otica setzt sich aus der Basalplatte, den beiden Ohrenkapseln und den Laminae supraoccipitales zusammen. Charakteristisch für sie sind die innige Verbindung mit der Occipitalregion, die schwache Verbindung mit der Orbitotemporalregion, die starke mediale Verlagerung der Schneckenkapsel (Fig. 34—36). Die Pars otica der Basalplatte, die den Boden der Oticalregion bildet, ist schon oben (S. 310—312) behandelt worden. Dass sie in ihrem rostralen Teil seitlich stark zusammengedrückt ist, steht in engster Beziehung zu der medialen Lagerung der rostroventralen Teile der Ohrenkapsel. Diese bilden nicht Boden des Cavum cranii, sondern fast ausschliesslich Seitenwände (Fig. 39—46) wie bei dem erwachsenen Tier. Das Verhältnis zwischen dem Volumen der Ohrenkapsel und dem der Schädelhöhle beträgt 1:25. Zur Vergrösserung der Seitenwand trägt die Hohe Lamina supracapsularis wesentlich bei, die etwa gleichmässig breit in weichem Bogen dorsal von der Ohrenkapsel und von dieser durch die Fissura capsuloparietalis (s. Foramen jugulare spurium) getrennt, entlangzieht (Fig. 34). Sie geht unvermittelt kaudalwärts in die schon beschriebene Cartilago supraoccipitalis über, rostralwärts bildet sie die wenig abgesetzte Lamina parietalis. Letztere verbindet sich durch die Commissura capsuloparietalis von vorn mit der Ohrenkapsel, ist aber in dieser Richtung sehr wenig entwickelt. Eine Commissura orbitoparietalis fehlt.

2. *Ohrenkapsel.*

Die mächtigen Ohrenkapseln werden am zweckmässigsten als annähernd nierenförmig beschrieben. Es können folglich zwei Pole, durch die die Längsachse zieht, sowie eine konvexe kaudale und eine konkave rostrale Kante unterschieden werden. Die Breite des Gebildes beträgt durchschnittlich 3/4 der

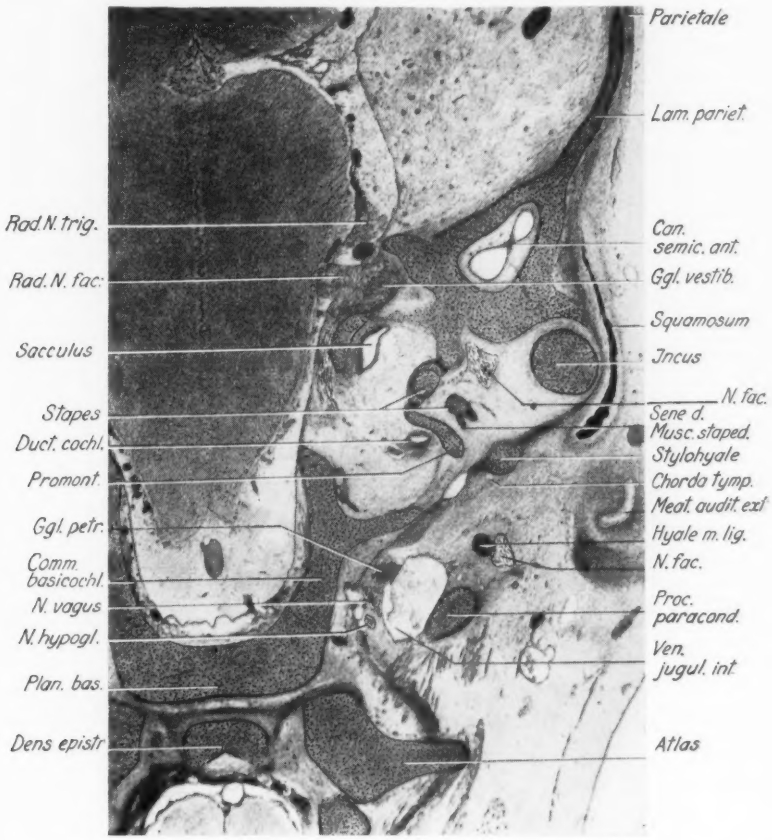

Fig. 41. Stad. XII. Schnitt durch Foramen acusticum superius. 20/1.

Länge. Zwei Teile der Ohrenkapsel — die dorsale, massigere Pars posterior s. canalicularis und die ventrale, schlankere Pars anterior s. cochlearis — grenzen sich ventral auf der Höhe des Foramen jugulare deutlich gegeneinander ab (Fig. 34—36). Jeder Teil nimmt etwa gleich viel von der totalen Länge der Ohrenkapsel in Anspruch, deren Längsachse sich von rostral, ventral und medial nach kaudal, dorsal und lateral streckt und mit der Ebene der Basalplatte einen Winkel von 60—65°, mit der Medianebene einen Winkel von etwa 23° bildet. Die grösste Ausdehnung der Ohrenkapsel senkrecht zu ihrer Längsachse erstreckt sich in der Pars canalicularis von rostral, dorsal und lateral nach kaudal, ventral und medial und bildet mit der Medianebene einen Winkel von 23—26°. In Pars cochlearis dagegen streckt sich die entsprechende Querachse von rostral, dorsal und medial nach kaudal, ventral und etwas lateral (Winkel mit der Medianebene etwa 15°). Im Zu-

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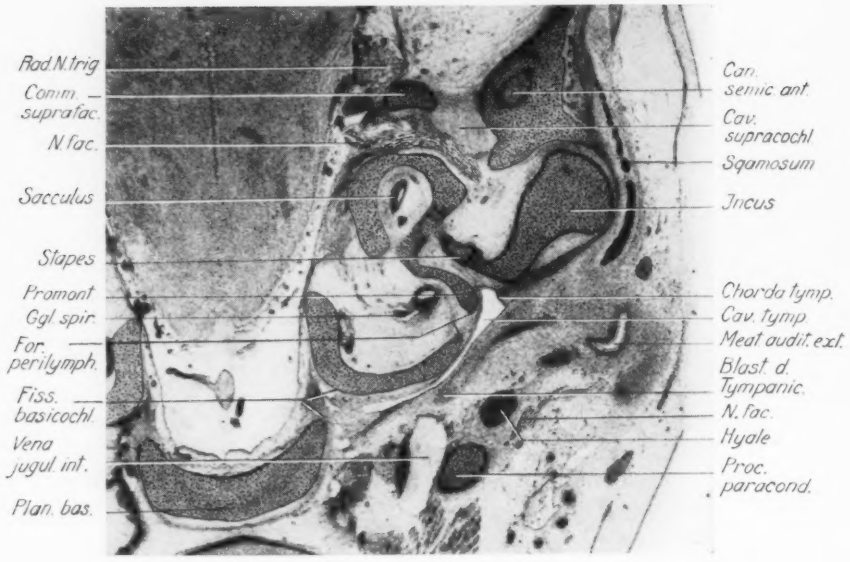

Fig. 42. Stad. XII. Schnitt durch Canalis facialis. 20/1.

sammenhang mit der verschiedenen Richtung der Querachse in den beiden Teilen der Ohrenkapsel entsteht an der Übergangsstelle zwischen beiden eine Konkavität der medialen Fläche. Diese bildet an der Pars cochlearis einen kleineren Winkel mit der Medianebene als an der Pars canalicularis. Der von den Ohrenkapseln und der Basalplatte eingeschlossene Raum hat im Gebiet der Commissura basicochlearis Trogform (Fig. 41), die aber rostralwärts immer mehr keilförmig im Querschnitt (Fig. 45) wird in dem Masse in dem die beiden Partes cochleares sich der Medianebene nähern. In ventraler Richtung ragt die Ohrenkapsel nicht über die Basalplatte hinaus (Fig. 34).

Die Ohrenkapsel steht an drei Stellen mit anderen Teilen des Chondrocraniums in homokontinuierlicher Verbindung. Die Commissura basicochlearis ist lang (Fig. 37) und erstreckt sich auf Grund der steilen Lage der Ohrenkapsel in einer etwa paramedialen Ebene (Fig. 41). Ihre Breite, d. h. ihre Ausdehnung in der Längsrichtung des Schädels, ist verhältnismässig klein. Sie entspricht einer Commissura basicochlearis posterior und wird hinten von dem Foramen jugulare, vorn von der Fissura basicochlearis begrenzt (Fig. 37). Diese, die kaudal ziemlich weit ist (Fig. 42—44) und rostralwärts, wo die Partes cochleares der Ohrenkapsel sich medialwärts vordrängen, allmählich sehr eng wird (Fig. 45, 46), trennt den rostralen Teil des Planum basale vollständig von der Ohrenkapsel. Eine Commissura basicochlearis anterior fehlt folglich. Die Pars canalicularis ist teils rostral durch die Commissura capsuloparietalis mit der Lamina parietalis, teils kaudal mit der

Lamina alaris und der Cartilago supraoccipitalis durch die sehr breite Commissura occipitocapsularis verbunden (Fig. 34, 37). Ihre ganze dorsale Kante wird dagegen durch die lange und ziemlich breite Fissura capsuloparietalis von der Lamina supracapsularis und der Cartilago supraoccipitalis getrennt.

Die Form der Pars canalicularis wird hauptsächlich durch den Verlauf der Bogengänge und die Streckung des Utriculus bedingt (Fig. 48). Etwas schematisiert kann man an der Pars canalicularis vier Flächen unterscheiden, die aber nur zum Teil sich gut voneinander abgrenzen lassen, nämlich eine rostroventrale, an deren medialen Teil sich die Pars cochlearis anschliesst, eine kaudoventrale, die die dorsale Begrenzung des Recessus jugularis und des Sulcus sigmoideus bildet, eine laterale und eine mediale Fläche, die an der freien dorsalen Kante der Ohrenkapsel entlang ineinander übergehen. Diese Kante wird zum grössten Teil von der scharf markierten Prominentia semicircularis anterior (s. superior) gebildet, mit derem rostralsten Teil sich die Commissura parietocapsularis verbindet. Eine Grenze fehlt hier an der medialen Fläche, ist aber an der lateralen als eine ganz leichte Einsenkung der Knorpeloberfläche wahrzunehmen (Fig. 34, 37). Rostral läuft die Prominentia semicircularis ventralwärts, erfährt eine scharfe Biegung nach kaudal und geht unmittelbar in die an der medialen Fläche erscheinende Prominentia utriculoampullaris superior über (Fig. 37). Diese Umbiegung tritt nur an der medialen Fläche der Pars canalicularis hervor, wo die Prominenz sich stark vorwölbt und sich von ventral gegen das Tegmen tympani gut absetzt. Die Modellierung der Knorpeloberfläche gibt den Verlauf des unterliegenden Bogenganges wieder (vgl. Fig. 48). An der lateralen Fläche ladet die Prominenz dagegen wenig aus und wird von dem Tegmen tympani teilweise überlagert. Die Prominentia semicircularis anterior geht kaudal von dem dorsalen Pol der Ohrenkapsel in die Prominentia semicircularis posterior über, die den kaudalsten Teil der dorsalen Kante der Ohrenkapsel bildet. Diese Prominentia biegt ventral um und stellt den kaudalen Rand der Pars canalicularis dar, mit der sich die Lamina alaris verbindet, und kann als ganz niedrige, ventralwärts und etwas lateralwärts ziehende Erhebung an der lateralen Fläche erkannt werden (Fig. 34). Über diese zieht die breite und kräftige Prominentia semicircularis lateralis etwa der dorsalen Kante der Pars canalicularis parallel. Nach hinten verschwindet sie in der Nähe der Prominentia semicircularis posterior, auf der sie hier etwa senkrecht steht, nach vorn läuft sie der kaudalen Ursprungsstelle des eigentlichen Tegmen tympani zu. Der von den drei durch die Bogengänge hervorgerufenen Prominentien umgebene Bezirk der lateralen Fläche blickt lateralwärts und etwas nach hinten. Er ist leicht konkav und enthält eine kleine Öffnung, die Durchbruchsstelle der Fossa subarcuata anterior (Fig. 34, 39). Eine zweite Öffnung, die ein Gefäss in die

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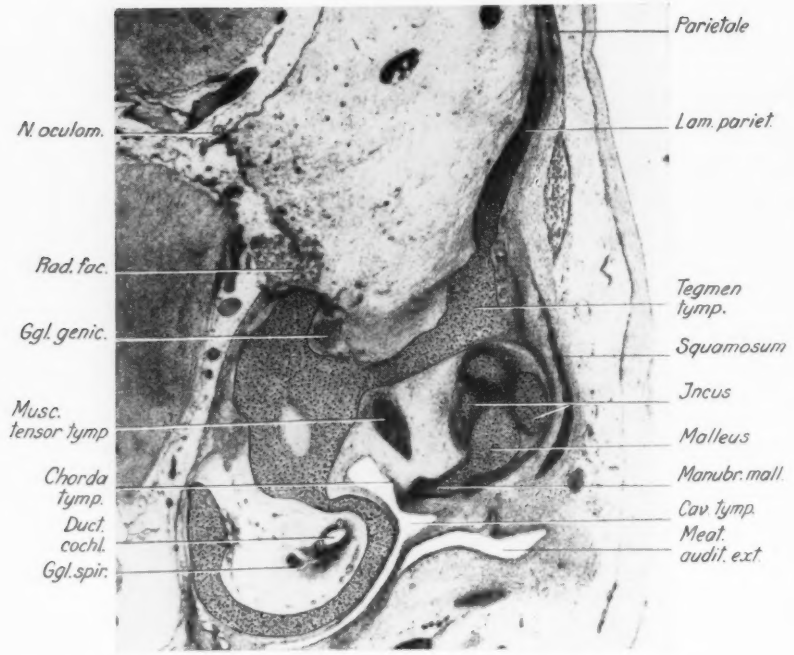

Fig. 43. Stad. XII. Schnitt durch das Incus-Malleus-Gelenk. 20/1.

Massa angularis durchlässt, findet sich in einer tiefen, trichterförmigen Einsenkung ventral von dem vordersten Teil der Prominentia semicircularis lateralis nahe dem vorderen Rand der lateralen Fläche (Fig. 34). Diese Einsenkung ist als Fossa subarcuata lateralis zu bezeichnen.

Die mediale Fläche (Fig. 37) der Pars canalicularis ist reicher modelliert als die laterale. Von dem Punkt an der dorsalen Kante, an dem die Prominentiae semicirculares anterior und posterior zusammenstossen, zieht die mächtige Prominentia cruris communis (s. sinus superioris) der Medianebene parallel der Basalplatte senkrecht zu. Rechtwinklig zu dieser Prominentia und also der Fissura capsuloparietalis parallel streckt sich die den Utriculus bergende Knorpelmasse. Nach rostral und dorsal endigt sie mit der Prominentia utriculoampullaris superior, nach kaudal und ventral mit der Prominentia utriculoampullaris inferior (Fig. 37). An der Stelle, wo die Prominentia cruris communis in diese Knorpelmasse übergeht, ist ihre Wand von einem kleinen ovalen Loch, dem Foramen endolymphaticum, durchbrochen, an das sich eine seichte, kaudalwärts ziehende Rinne anschliesst. In dieser Rinne verläuft das Endstück des durch das Foramen endolymphaticum durchtretenden Ductus endolymphaticus, der in einem flachen, langgestreckten Saccus endolymphaticus

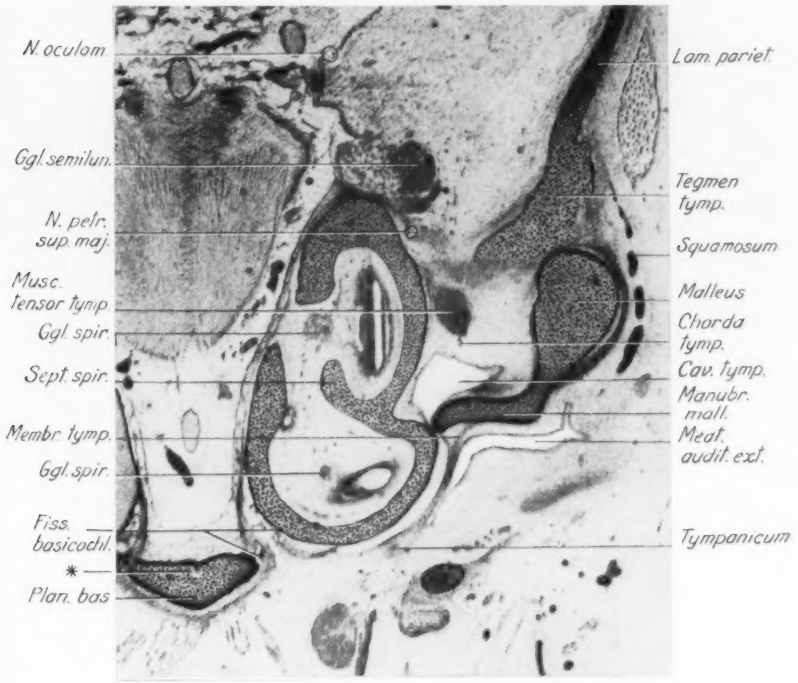

Fig. 44. Stad. XII. Schnitt durch Manubrium mallei. 20/1.

endigt (Fig. 48). Dieser liegt kaudal von der Prominentia cruris communis. Auch rostral von dem Foramen endolymphaticum beeinflusst der Ductus endolymphaticus die Form des Knorpels, indem sein Verlauf innerhalb der Kapsel sich durch eine kleine Erhebung an der Knorpelwand abzeichnet.

Durch die Prominentia cruris communis wird die mediale Fläche der Pars canalicularis in ein vorderes und ein hinteres Gebiet geteilt. Die medial-vordere Fläche wird hinten von der Prominentia cruris communis und dorsal von der prominentia semicircularis anterior begrenzt. Nach vorn dehnt sie sich bis über den scharf umgebogenen ventralen Teil der Prominentia semicircularis anterior und über die Prominentia utriculoampullaris superior aus, und ventral geht sie ohne sichtbare Grenze in die mediale Begrenzung der Schneckenkapsel über. Die betreffende Fläche bildet einen Winkel von etwa 35° mit der Medianebene (Fig. 34), stellt also einen Teil der Wand des Cavum cranii dar. Nur über die Prominentia utriculoampullaris anterior und den umgebogenen Teil der Prominentia semicircularis anterior neigt sie sich stärker lateralwärts (Fig. 40, 41) und bildet Boden. Sie wird zum grossen Teil von einer tiefen Fossa subarcuata anterior eingenommen (Fig. 37). Diese, die die Form eines gleichschenkligen Dreiecks hat mit dem einzigen spitzen Winkel kaudal-

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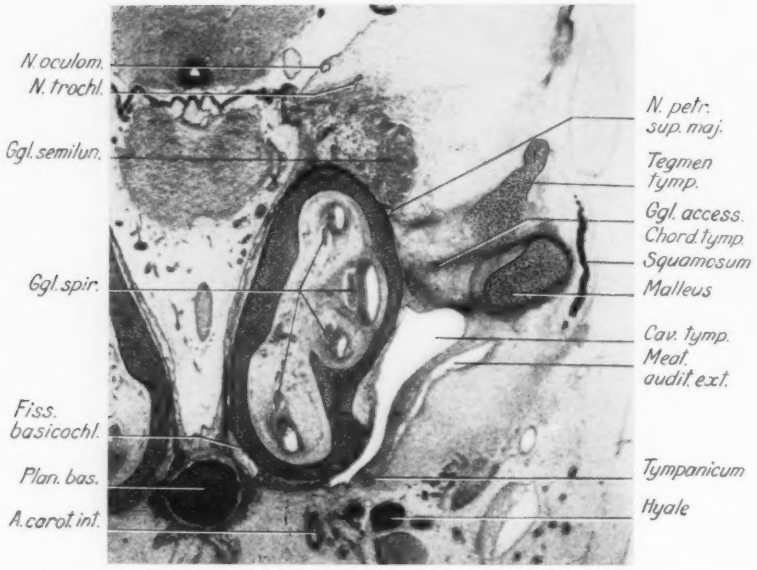

Fig. 45. Stad. XII. Schnitt durch den mittleren Teil der Schneckenkapsel. 20/1.

wärts gerichtet, streckt sich als trichterförmige Vertiefung durch etwa 2/3 der Knorpellamelle, verläuft aber dann als gleichmässig weiter Kanal bis zu der lateralen Oberfläche. Sie ist von einer dicken, medial konkaven Bindegewebsmembran abgeschlossen, die die Fortsetzung des Perichondriums ausmacht und von zahlreichen kleineren Blutgefässen durchbrochen wird (Fig. 39). Die Fossa ist mit lockerem Bindegewebe gefüllt. Nur ein einziges der genannten Gefässe dringt durch den Kanal durch und verzweigt sich auf der lateralen Fläche.

Die medial-hintere, von den Prominentiae cruris communis und semicircularis posterior begrenzte Fläche steht vorn der Medianebene parallel, ist weiter kaudalwärts nach hinten gerichtet, um schliesslich kaudodorsal von der Prominentia utriculoampullaris inferior wieder medialwärts und etwas ventralwärts zu blicken. Hierdurch bildet die medial-hintere Fläche kaudal eine nach medial und hinten schauende Konkavität (Fig. 37), die von dem Sinus sigmoideus durchzogen wird und den Saccus endolymphaticus aufnimmt.

In der Längsrichtung des Schädels ist die kaudoventrale Fläche der Pars canalicularis kurz. Sie stellt die Decke von Recessus jugularis und Sulcus sigmoideus dar und geht medialwärts und kaudalwärts in die medial-hintere Fläche über. Im Gebiete des Sulcus sigmoideus enthält sie eine sich medial von der Prominentia semicircularis posterior trichterförmig vertiefende Grube, die Fossa subarcuata posterior, die von einem in das Innere des Knorpels führenden Kanal fortgesetzt wird. Durch den Sulcus sigmoideus,

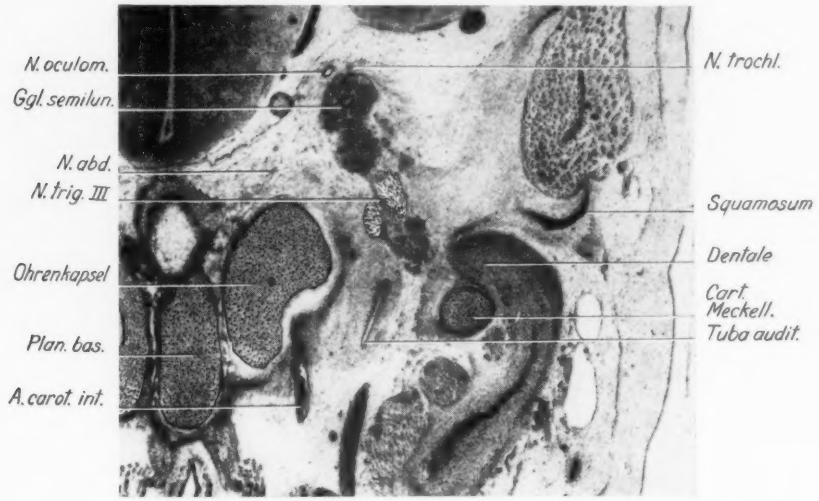

Fig. 46. Stad. XII. Schnitt durch den vordersten Teil der Schneckenkapsel. 20/1.

dessen laterale Begrenzung dorsal von der Prominentia semicircularis posterior, ventral von der Lamina alaris gebildet wird (Fig. 39), zieht der Sinus sigmoideus nach vorn, um in dem Gebiet des Recessus jugularis in die Vena jugularis interna überzugehen.

Im Inneren der Massa angularis, die zwischen den Bogengängen eingeschlossen ist, findet sich ein ziemlich grosses Gebiet, in dem die Knorpelgrundsubstanz aufgelöst worden ist, und in dessen Peripherie diese sich im Abbau befindet (Fig. 39). Die so entstandene Höhlung ist mit lockerem Bindegewebe und einem aufgelockerten Knorpelgewebe gefüllt und streckt sich von der Gegend der Fossa subarcuata anterior zu dem kaudalen Teil des Sulcus sigmoideus. Durch sämtliche drei Fossae subarcuatae ziehen Gefässe in das Innere der Massa angularis hinein.

Die rostroventrale Fläche der Pars canalicularis zeichnet sich durch konkave Form und mehrere nach vorn und ventral gerichtete Fortsätze aus (Fig. 36). Die Konkavität wird zunächst durch die leichte Biegung des Utriculus nach dorsal und das Vorspringen der Ampulla anterior und Ampulla posterior nach ventral verursacht, vor allem aber durch die ventralwärts gerichtete, scharfe Umknickung des vorderen und hinteren Bogenganges (Fig. 48). Noch weiter accentuiert wird sie durch das rostralwärts sich streckende Tegmen tympani.

Als grösster und auffälligster Fortsatz der ventrorostralen Fläche der Pars canalicularis können wir Pars cochlearis auffassen, die etwas weniger als die Hälfte der genannten Fläche in Anspruch nimmt. Die Pars cochlearis hat grob die Form eines bikonvexen Linsensegmentes, dessen Schnittfläche sich gegen die Pars canalicularis wendet. Nach vorn wird sie etwa auf der

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Höhe der Crista transversa kuppelförmig abgeschlossen und lässt deutlich zwei Abschnitte erkennen (Fig. 34). Der hintere, Pars vestibularis (VOIT 1909) enthält hauptsächlich den Sacculus und den geraden Teil des Ductus cochlearis, während der vordere, „Pars cochlearis" in engerem Sinne, nur den aufgewundenen Teil des Schneckenganges birgt.

Die laterale Fläche der Pars vestibularis zeigt eine markante Furche, den Sulcus vestibularis, die in Seitenansicht mit der Längsachse des Schädels zusammenzufallen scheint, in Wirklichkeit aber sich der Medianebene nach vorn zu nähert und mit dieser einen Winkel von etwa 19° bildet. Zu beiden Seiten dieser Furche, die eine kaudale Verlängerung des hinten tiefen, weiter nach vorn ganz seichten Sulcus septalis darstellt (Fig. 47), wölbt sich die Wand lateralwärts hervor. Ventral bildet sie das stark hervortretende Promontorium (Fig. 47), dorsal eine weniger weit vorspringende Vorwölbung, die den Sacculus birgt und nach vorn gegen die eigentliche Schneckenkapsel, nach hinten gegen die Pars canalicularis stösst. Diese Wölbung zeigt an der ventralwärts und etwas nach vorn schauenden Fläche eine ovale Öffnung, die Fenestra vestibuli (Fig. 47), die, sich über die ganze Pars vestibularis erstreckend, fast doppelt so lang wie breit ist, und deren ventraler Rand hinten mit dem Sulcus vestibularis zusammenfällt, weiter nach vorn aber durch einen schmalen Knorpelstreifen von diesem getrennt ist.

Auf das Promontorium folgt ventrokaudal eine grosse Öffnung, (Fig. 42) das Foramen perilymphaticum, die nicht in einer Ebene liegt, sondern aus einer Cylinderfläche ausgeschnitten ist. Demzufolge blickt sie vorn lateral, hinten dagegen, wo sie sich weiter medial ausdehnt, lateral und ventral. Der dorsale Rand des Foramen perilymphaticum läuft etwa dem Sulcus vestibularis parallel und hört kaudal an der vorderen Fläche der Pars canalicularis auf. Der ventrale Rand, der grösstenteils von dem Boden der Pars vestibularis gebildet wird, zieht von vorn lateral nach hinten medial und stösst auf die mediale Wand der Pars vestibularis an der Stelle, wo diese sich mit dem hintersten Teil der Commissura basicochlearis gerade vor dem Foramen jugulare verbindet. Sie verläuft aber nicht gerade, sondern ihr vorderer und hinterer Teil bilden einen stumpfen Winkel. Hierdurch entsteht ein breiter laterokaudal und etwas dorsal gerichteter Fortsatz, der Processus infraperilymphaticus (FISCHER 1903, VOIT 1909) oder recessus (DE BEER 1930). Die hintere Begrenzung des Foramen perilymphaticum bildet den ventralsten Teil der vorderen Fläche der Pars canalicularis, die sich hier als kleine Prominentia nach vorn wölbt. Diese formt sich zu einem kleinen, nach vorn gerichteten, dem Processus recessus gegenüberstehenden Fortsatz. Die Aufteilung des Foramen perilymphaticum in die laterale Fenestra cochleae (Foramen rotundum) und den medianen Aquaeductus cochleae hat also schon angefangen. Das Foramen perilymphaticum ist

von einer festen Bindegewebsmembran verschlossen, die zum Teil zur Membrana tympani secundaria wird. Diese Membran schliesst sich nicht der Kante des Promontorium an, sondern dessen ventraler Fläche, etwas von der Kante zurückgezogen (Fig. 40—42). In dem medial-hinteren Teil des Foramen senkt sie sich abwärts und stülpt sich als kurzer Saccus perilymphaticus vor (Fig. 40), dessen mediale Wand von einer kleinen Vene durchbohrt wird. Diese wird von einer anderen kleinen aus dem Cavum cranii kommenden und in die Vena jugularis mündenden Vene aufgenommen, auf die wir unten zurückkommen.

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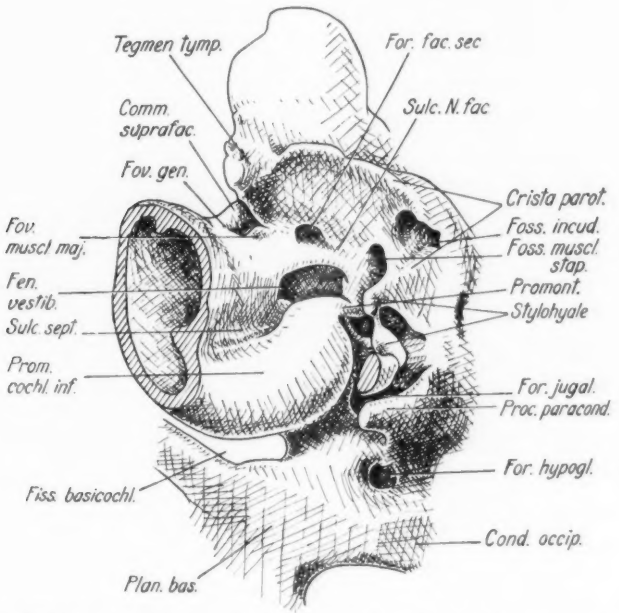

Fig. 47. Stad. XII. Rostroventrale Fläche der Pars canalicularis von ventral und vorn gezeichnet. 15/1.

Das Promontorium setzt sich in dem dorsalen Teil der Prominentia cochlearis inferior nach vorn fort (Fig. 47), die in einem weiten spiralförmigen Bogen allmählich von der lateralen auf die ventrale Fläche der Schneckenkapsel übergeht, um schliesslich in dessen Cupula sich zu verlieren (Fig. 34). Begleitet wird diese Prominentia von dem Sulcus septalis, der in seinem vorderen, seichten Teil die Ansatzlinie des im Inneren vorspringenden Septum spirale markiert. Vorn vereinigt sich der Sulcus septalis mit einer angedeuteten Furche (Fig. 35), dem Sulcus caroticus, der an der Cupula der Schneckenkapsel von ventrolateral nach dorsomedial ansteigt und die Arteria carotis interna aufnimmt (Fig. 46). Dorsal von dem Sulcus septalis wölbt sich die laterale Fläche der Schneckenkapsel nochmals als eine grosse Prominentia cochlearis superior hervor (Fig. 34), die

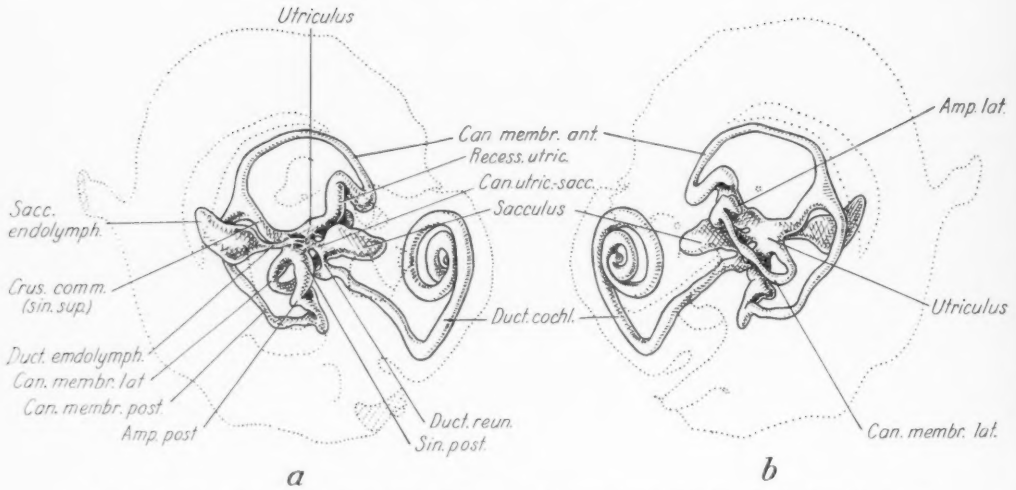

Fig. 48. Stad. XII. Projektion des Labyrintes in Beziehung zu der Ohrenkapsel. *a* von medial; *b* von lateral. 10/1.

der zweiten und dritten Windung des Ductus cochlearis entspricht. Eine ganz flache Einbuchtung am ventralen und rostralen Teil der letztgenannten Prominentia gibt die Ansatzlinie des hier bindegewebigen, zwischen der zweiten und dritten Windung des Ductus cochlearis vorspringenden Teils des Septum spirale an.

An dem ganzen freien Umkreis der eigentlichen Schneckenkapsel geht die laterale Fläche mit rundlicher Wölbung in die mediale über. Dasselbe gilt für den vorderen ventralen Teil der Pars vestibularis, während hinten der Übergang der beiden Flächen ineinander durch das Ansetzen der Commissura basicochlearis unterbrochen wird. Dorsal gestaltet sich die Pars vestibularis sehr kompliziert durch die Ausbildung von Foramina und Commissuren.

Die mediale Fläche der Pars cochlearis zeigt im vorderen Teil rundliche Wölbung, im hinteren vestibularen Teil dagegen leichte Konkavität. Das Foramen acusticum inferius, das den unteren Acusticusast durchlässt, streckt sich etwa in der Längsrichtung des Schädels nach hinten bis zu der Pars canalicularis und dehnt sich über die vier hinteren Siebentel der Pars cochlearis aus (Fig. 37). Es ist anderthalbmal länger als seine Breite beträgt. Sein scharf abgesetzter ventraler Rand schreibt einen tiefen nach ventrokaudal konvexen Bogen. Der dorsorostrale Rand dagegen verläuft verhältnismässig gerade. Die vordere Hälfte letzterer setzt sich nicht scharf ab, sondern die Kapselwand sinkt hier allmählich in das Innere hinein und geht durch Drehung in eine kräftige, transversal gestellte Querwand, Septum metacochleare (MATTHES 1921), über, die den cochlearen von dem vestibularen Hohlraum trennt (Fig. 37). Dieses Septum biegt in seinem ventralen Teil

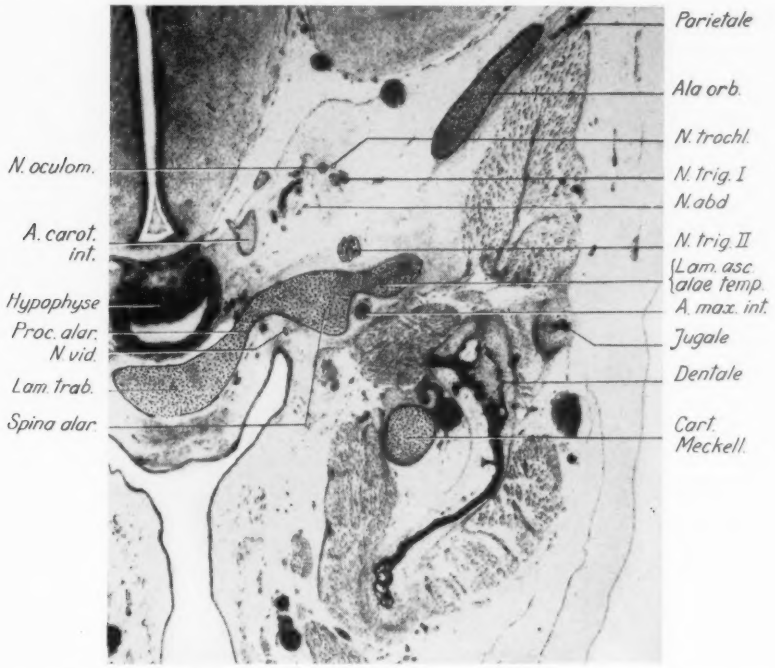

Fig. 49. Stad. XII. Schnitt durch den hinteren Teil des Processus pterygoideus medialis. 20/1.

rostral um und setzt sich rostralwärts in das Septum spirale cartilaginum fort. Der hintere Teil des betreffenden Randes setzt sich wiederum scharf ab bis auf einen hintersten kleinen Streifen, wo die Kapselwand wieder allmählich in das Innere hineinsinkt und durch Drehung eine kleine unvollständige, sagittalstehende Scheidewand bildet. Von der Medianebene sieht man rostral von dem Septum metacochleare durch das Foramen acusticum inferius in das Cavum cochleare hinein (Fig. 37).

Dorsorostral von dem behandelten Foramen findet sich eine Nische von etwa ovalem Umriss und grösster Ausdehnung in der Längsrichtung des Schädels. Ihre dorsorostrale Begrenzung kommt durch die Commissura suprafacialis zustande (Fig. 37), die als runde, leicht gebogene Knorpelspange sich von dem kaudalsten Teil der Decke der eigentlichen Schneckenkapsel zu der Grenze zwischen Pars vestibularis und Pars canalicularis, also über erstere hinweg wölbt. Die beiden kräftigeren Endstücke dieser Spange sind mit breiter Basis befestigt. In der Nische sind zwei Öffnungen vorhanden, kaudal das Foramen acusticum superius, das ventrokaudal von der hinteren Ansatzstelle der Commissura suprafacialis in die Pars canalicularis führt (Fig. 35, 37) und den oberen Acusticusast durchlässt, rostral das von

der genanten Commissur und der darunterliegenden Decke der Pars vestibularis umgrenzte Foramen faciale oder der primäre Facialiskanal (Fig. 37, 42, 47). Der die beiden Foramina acustica trennende Knorpelstreifen, der den vorderen Teil des Sacculus birgt (Fig. 41), ist nicht eingesunken. Es fehlt also hier eine langgestreckte Grube im Gebiet der beiden Foramina acustica, die bei anderen Säugern das Ganglion vestibulare aufnimmt und die Anlage des Meatus acusticus internus darstellt. Dagegen zieht sich die Kapselwand zwischen dem Foramen faciale und dem Foramen acusticum inferius zu einer flachen Rinne zurück.

Als nächst grösster Fortsatz entspringt Tegmen tympani im engeren Sinne dem vordersten Gebiet der rostroventralen Fläche der Pars canalicularis, d. h. dem scharf umgebogenen Teil der Prominentia semicircularis anterior (Fig. 34, 37, 47). Sein vorderster Teil stellt eine dicke, etwas abgeknickte Platte dar, die ventral dicker ist und eine ventrolaterale und eine dorsomediale Fläche zeigt, die dorsal dünner ist und hier der Medianebene parallel steht. Das vorderste Drittel dieser Platte steht frei hervor und ist mit mehreren kleinen Auswüchsen und Unebenheiten besetzt. An den zwei hinteren Dritteln der betreffenden Platte kann erkannt werden, dass die Lamina parietalis an deren Aufbau beteiligt gewesen ist (Fig. 44). Diese schliesst sich hier, den vordersten Teil der Commissura capsuloparietalis bildend, von medial her der Platte an, aus deren histologischer Struktur immer noch ersichtlich ist, dass zwei aneinander liegende Knorpelplatten miteinander verschmolzen sind. In seinem dorsalen Teil geht Tegmen tympani mit einer in Lateralansicht deutlichen Grenze in die Lamina parietalis über, d. h. hier hört die laterale Komponente auf (Fig. 44). Auch der ventrale Teil des Tegmen tympani wird in kaudaler Richtung dünner, breitet sich gleichzeitig mit einer Drehung von der Medianebene sowohl medial- wie lateralwärts aus und schmiegt sich dem vorderen Teil der rostroventralen Fläche von Pars canalicularis an. Ihre vorn lateroventralwärts blickende Fläche wird hierdurch weiter nach hinten leicht konkav nach ventral gerichtet (Fig. 47). Die mediale Kante des Tegmen tympani verschmilzt, von dem Foramen faciale secundarium (s. externum) durchbohrt, mit der seitlichen Decke der Pars vestibularis. Der Ansatz der so entstandenen Commissur ist ziemlich breit. Seine rostroventral gewandte Fläche zeigt am Übergang in die Ohrenkapsel eine kleine, seichte Eindellung (Fig. 47), die Fovea muscularis major, die Ansatzstelle des Musculus tensor tympani.

Lateral von der Commissura suprafacialis findet sich ein Teil der Schädelhöhle als Cavum supracochleare, das in Dorsalansicht rombische Form hat mit einem stumpfen Winkel kaudalwärts gerichtet (Fig. 36). Nach hinten wird es medial von der Commissura suprafacialis und lateral von der Prominentia semicircularis anterior begrenzt und ist hier scharf abgesetzt. Nach vorn kommt seine Begrenzung medial durch die laterale Fläche der Pars

cochlearis und lateral durch die mediale Fläche des Tegmen tympani zustande, jedoch in beiden Fällen wenig ausgeprägt und ohne vollständigen Abschluss des Cavum supracochleare nach vorn. Es setzt sich hier in das Cavum epiptericum fort. Der Boden des Cavum supracochleare wird medial von der lateralen Decke der Pars vestibularis, lateral von dem medialen Teil des Tegmen tympani gebildet. Er steht der Basalplatte etwa parallel und wird in seinem kaudalsten Teil von dem ventrokaudal gewandten Foramen faciale secundarium durchbohrt (Fig. 42). — Das Cavum supracochleare ist mit Bindegewebe gefüllt und wird von dem N. facialis durchzogen, dessen Ganglion geniculi grösstenteils in dem rostralen Teil der lateralen Mündung des kurzen Canalis facialis primarius liegt. Dieses Ganglion streckt sich rostralwärts und gibt den Ramus petrosus superfacialis ab. Hierbei durchzieht es in Bindegewebe eingebettet ein kleines, leicht vertieftes Gebiet (Fig. 47), die Fovea genicularis, die an der lateralen Fläche der rostralen Wurzel der Commissura suprafacialis entlangläuft.

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Die laterale Kante des hinteren Teiles von Tegmen tympani zieht in einem ventralwärts offenen Bogen als gesimsartig vorstehende Crista parotica nach hinten und stellt eine auffällige Grenze zwischen der lateralen und der rostroventralen Fläche der Pars canalicularis dar (Fig. 34, 47). Sie fängt vorn eben da an, wo der hintere Teil des Tegmen tympani in den vorderen übergeht und stellt eine Fortsetzung der Kante dar, die durch die Abknickung der Platte des vorderen Teiles entstanden ist (vgl. S. 328). Lateral von dem kaudalen Rand der in rostrokaudaler Richtung gestreckten Mündung des Foramen faciale secundarium (Apertura tympani canalis facialis) ist ihre laterale Kante auf einer kleinen Strecke schwach ausgebildet (Fig. 34, 47). Die Verbindungslinie zwischen dieser Stelle und dem hinteren Rand des äusseren Foramen faciale gibt die hintere Grenze des eigentlichen Tegmen tympani an.

Die kaudalwärts folgende Fortsetzung der ventralen Fläche des Tegmen tympani, die in weiterem Sinne diesem zuzurechnen ist, wird von der rostroventralen Fläche der Pars canalicularis gebildet. Dasselbe gilt für das kaudalwärts folgende Stück der Crista parotica, die einen scharfen Bogen macht, sodass ihr hinterster Teil ventral- und etwas medialwärts zieht. Dieser Teil der Crista parotica springt als im Querschnitt dreieckige Platte in der Längsrichtung des Schädels vor (Fig. 34, 35, 40, 47). Mit ihm verbindet sich von vorn das proximale Ende des Stylohyale.

Von dem kaudalen Ende der Apertura tympani canalis facialis zieht eine sehr seichte Furche, der Sulcus facialis, kaudalwärts der rostrodorsalen Kante der Fenestra ovalis parallel (Fig. 47). Ihre laterale Begrenzung, eine breite, niedrige Erhöhung, die einer Crista facialis entspricht, setzt sich so wenig ab, dass sie kaum als Crista angesprochen werden kann. Zwischen ihr und der Crista parotica zeigt die Oberfläche eine leichte Konkavität, die

eine seichte und wenig ausgebreitete Fovea epitympanica darstellt. Diese vertieft sich nach hinten unvermittelt zu einer Fossa incudis, die das Crus breve incudis aufnimmt und nach lateroventral offen steht (Fig. 34, 47). Hierdurch geht die Kontinuität der Crista parotica verloren. Medial von dem kaudalsten Teil von dieser findet sich eine grosse, tiefe Grube (Fig. 40, 47), Fossa musculi stapedii (Fossa muscularis minor), die sich medial bis zu dem kaudalen Ende der Fenestra vestibuli streckt und sowohl, rostralwärts wie ventralwärts offen ist (Fig. 36, 40, 47). Sie nimmt den Musculus stapedius auf, der an der medialen Fläche des kaudalen Teils der Crista parotica ansetzt (Fig. 40). Ihre Mündung wird von dem Nervus facialis überquert.

Der ventralste Teil der rostroventralen Fläche von Pars canalicularis ist flach und geht über den dorsalen Rand des Foramen jugulare in die kaudoventrale Fläche der Pars canalicularis über. In einigem Abstand von der Mitte findet sich eine breite, niedrige Vorwölbung, die den ventralen, scharf abgeknickten Teil des hinteren Bogenganges birgt. Sie ist als kleiner Fortsatz ausgebildet und nimmt an der Aufteilung des Foramen perilymphaticum teil.

3. *Die Kavitäten der Ohrenkapsel.*

Der Binnenraum der Ohrenkapsel zeigt die typische Gliederung in Cavum canaliculare, Cavum vestibulare und Cavum cochleare. Als zentraler Hohlraum füllt das Cavum vestibulare den vestibularen Teil der Schneckenkapsel aus und steht rostral mit dem Cavum cochleare, kaudal mit zwei grossen Aussackungen, dem dorsalen Recessus utriculoampullaris superior und dem ventralen Recessus utriculoampullaris inferior in Verbindung. Die beiden Recessus werden voneinander durch eine von der lateralen Wandung einbuchtende Knorpelmasse getrennt. Auch der dorsale Teil des Cavum vestibulare ist durch eine Einbuchtung der lateralen Wand eingeengt. In diese Abteilung führen Fenestra vestibularis, Foramen acusticum superius und der dorsokaudale Teil des Foramen acusticum inferius, während der ventrokaudale Teil desselben Foramen wie das Foramen perilymphaticum in die geräumigere ventrale Abteilung des Cavum vestibulare führen. Die dorsorostrale Abteilung des Cavum vestibulare wird durch das rostralwärts konkave Septum metacochleare, das in der Mitte ein spät geschlossenes, immer noch aus vorknorpeligem Gewebe bestehendes Gebiet enthält, vollständig von dem Cavum cochleare getrennt. Das betreffende Septum zeigt aber auch eine nach kaudalwärts gerichtete Konkavität, in die sich das rostrale Ende des Sacculus hineinstreckt (Fig. 42). Dieser zieht wie gewöhnlich in rostroventraler Richtung dem Knorpelstreifen zwischen den Foramina acustica entlang (Fig. 41).

Die kaudale Begrenzung der geräumigen Abteilung des Cavum vestibulare fasse ich als einen Teil der rostroventralen Fläche der Pars canalicularis auf,

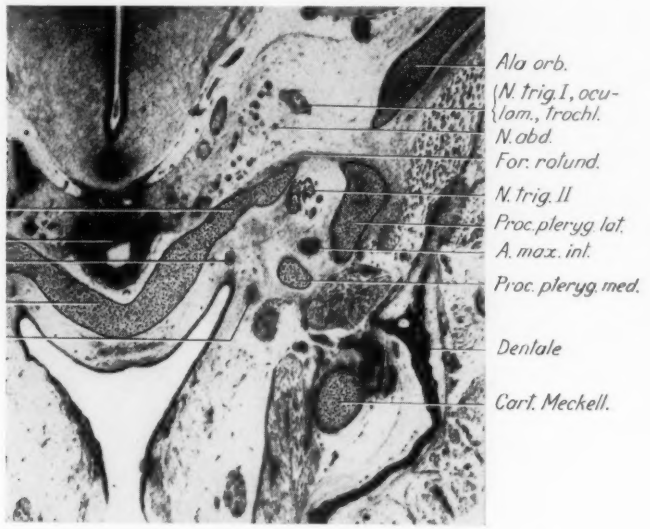

Fig. 50. Stad. XII. Schnitt durch Foramen rotundum. 20/1.

da sie durch die Ausbildung des grossen Foramen perilymphaticum eine direkte Fortsetzung der betreffenden Fläche darstellt. In dieser findet sich medial und etwas rostral von der oben beschriebenen kleinen Vorwölbung die Mündung eines kurzen Kanals, die in lateraler Richtung in den Recessus utriculoampullaris posterior führt und einen Ast der Radix vestibularis zusammen mit einer kleinen Vene durchlässt. Mit dieser vereinigen sich andere kleinste Venen, die das Cavum cranii durch den kaudalsten Teil des Foramen acusticum inferius verlassen und als etwas grössere Vene aus dem Cavum vestibulare medial von dem Saccus perilymphaticus durch das Foramen perilymphaticum tritt und in die Vena jugularis einmündet. Der betreffende Nerv (Ramus ampullaris posterior) zieht nicht frei durch das Cavum vestibuli, sondern verläuft in einem nach laterodorsal und auch — obwohl weniger vollständig — nach rostral abgeschlossenen kleinen Raum, der durch das Einsinken der dorsorostralen Kante des Foramen acusticum inferius abgeteilt worden ist (vgl. oben). Lateral von dieser kleinen Scheidewand öffnet sich der Recessus utriculoampullaris inferior nach hinten. Dieser wie der Recessus utriculoampullaris superior sind in typischer Weise ausgebildet und enthalten die entsprechenden Abschnitte des häutigen Labyrinths. Es sei nur bemerkt, dass der Ductus endolymphaticus von seinem Ursprung an bis zu seinem Austritt aus der Ohrenkapsel durch das Foramen endolymphaticum von einer Rinne in der medialen Kapselwand begleitet wird (Fig. 39).

Der mit einem ziemlich grossen Vorhofsblindsack dorsal endende Ductus cochlearis zieht der ventralen Fläche des Promontorium angeschmiegt (Fig.

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41, 42) ventralwärts und nimmt grösseren Durchschnitt bei seinem Eintreten in das Cavum cochleare an. Die Kommunikation zwischen diesem und dem Cavum vestibulare ist ventral weit, dorsal aber stark eingeengt und fast spaltförmig (Fig. 44). Diese Einengung ist sowohl durch die Form der Schneckenkapsel wie durch die Verdickungen ihrer Wandung bedingt: 1) die zweite Windung der Schneckenkapsel ist medialwärts in den Raum der ersten Windung gedrückt und bildet in Zusammenhang hiermit einen wesentlich kleineren Winkel mit der Medianebene als die erste Windung. 2) Eine wulstförmige Verdickung an der Innenseite des ventralen Randes von Foramen acusticum inferius umzieht das rostrale Ende des betreffenden Foramen, geht auf dessen dorsalen Rand und schliesslich auf die rostrale Kante des Septum metacochleare über (Fig. 44). Das aus jungem Knorpelgewebe bestehende Septum spirale zieht, immer niedriger werdend, als Fortsetzung dieser Kante weiter rostralwärts und schliesslich dorsalwärts und durchläuft etwa zwei Drittel einer Windung. Die Anlage eines Modiolus ist noch nicht ausgebildet. Auch von den beiden Scalae ist noch keine Andeutung vorhanden. — Der Ductus cochlearis macht im ganzen 2 1/2 spiralförmige Windungen durch (Fig. 48).

Auf das Cavum canaliculare, das keine Besonderheiten aufweist, wird nicht näher eingegangen. Die Anordnung der Räume für die Bogengänge geht bereits aus Fig. 48 hervor und kommt in der äusseren Form der Ohrenkapsel zum Ausdruck (s. oben).

Sämtliche Teile des häutigen Labyrinths sind allseits durch lockeres Bindegewebe von der Knorpelwänden getrennt. Die Ausbildung eines zusammenhängenden perilymphatischen Hohlraumes hat nirgends eingesetzt.

4. *Nerven und Blutgefässe der Regio otica.*

Nervus vagus, Nervus glossopharyngeus und Nervus accessorius verlassen das Cavum cranii durch das Foramen jugulare, wobei Nervus vagus ventral von Nervus glossopharyngeus verläuft. Nervus vagus bildet im Recessus jugularis das Ganglion jugulare (Fig. 39) und gibt hier seinen Ramus auricularis ab. Dieser zieht nach dem Durchtreten durch das Foramen jugulare lateral und vereinigt sich mit dem Nervus facialis, eben wo dieser ventral von dem Reichertschen Knorpel nach vorn umbiegt. Dicht an das Ganglion jugulare gedrückt findet sich dorsal hiervon im Recessus das Ganglion superius nervi glossopharyngei (Fig. 39). Dieser Nerv bildet sein Ganglion petrosum (s. distale) erst nach dem Austritt durch das Foramen jugulare. Das proximale Ende dieses Ganglion entsendet einen ziemlich starken Nervenast, der wie der Ramus auricularis vagii ventral von der Vena jugularis lateralwärts zieht und sich eng an den Hauptstamm des Nervus facialis anschmiegt. Es dürfte sich hier um einen Ramus communicans n. facialis et

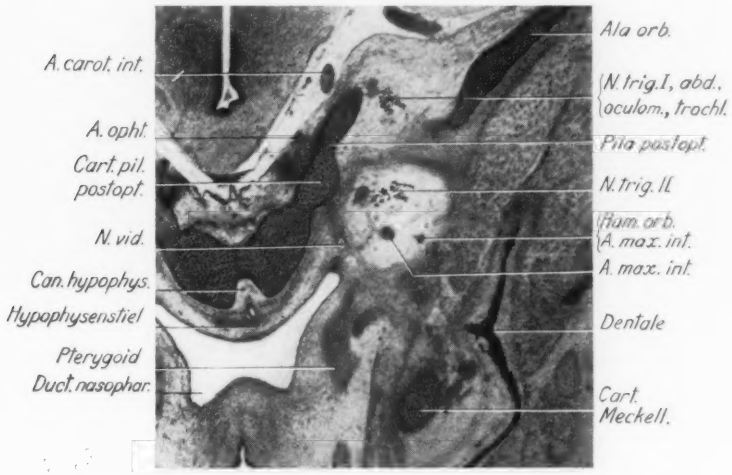

Fig. 51. Stad. XII. Schnitt durch Cartilago pilae postopticae. 20/1.

glossopharyngei handeln. Der sehr feine Nervus tympanicus konnte in der betreffenden Schnittserie nicht verfolgt werden. Die folgende Beschreibung bezieht sich deswegen auf das Stadium von 22 mm Länge. Der Nervus tympanicus verlässt das Ganglion etwas weiter distal, zieht ventral von der Prominentia cochlearis inferior rostralwärts, passiert entlang der ventralen Begrenzung des Cavum tympani und biegt hierbei allmählich etwas dorsal um. Er bildet gerade gegenüber von dem Sulcus septalis ein kleines Ganglion tympanicum, läuft dann zwischen dem Cavum tympani und der lateralen Ohrenkapselwand rostrodorsal und bildet dicht an dieser, medial von dem ventralen Rand des Meckelschen Knorpels ein zweites kleines Ganglion. Weiter habe ich diesen Nerv nicht verfolgen können. Auch eine Verbindung zwischen dem Nervus tympanicus und dem Ramus auricularis vagi liess sich nicht auffinden.

Die beiden Wurzeln des Nervus acusticus, Radices cochlearis et vestibularis, verlassen getrennt das Gehirn rostral und in der Nähe von Foramen endolymphaticum. Radix vestibularis bildet unmittelbar das grosse, einheitliche, gegen die mediale Fläche der Ohrenkapsel flachgedrückte Ganglion vestibulare. Dieses ist langgestreckt in der Richtung dorsorostral — ventrokaudal, dehnt sich im dorsalen Teil von dem ventralen Rand der Fossa subarcuata anterior hinten bis über das Foramen acusticum superius nach vorn aus, dessen dorsalen Teil es abschliesst (Fig. 41). Nach ventral allmählich schmäler werdend, streckt sich das Ganglion über den dorsalen Rand des Foramen acusticum inferius, mit seinem Ende hinter dem Septum metacochleare zipfelartig hineinhängend. Radix cochlearis zieht zunächst ventralwärts am kaudalen Rand des Ganglion vestibulare entlang, läuft dann quer über dessen mediale Fläche, fängt an, spiralig auszustrahlen und setzt sich

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rostralwärts auf der medialen Fläche des Septum metacochleare fort. Sie bildet wie gewöhnlich längs des konkaven Randes des Ductus cochlearis das Ganglion spirale. Die einzelnen Zweige des Nervus acusticus verteilen sich folgendermassen auf die Foramina:

For. Acusticum sup.:
1. Ramus ampullaris ant.,
2. Ramus ampullaris lat.,
3. Ramus utricularis,
4. Ramus saccularis sup.,

For. Acusticum inf.:
1. Ramus saccularis post.,
2. Ramus ampullaris post.,
3. Radix cochlearis.

Ramus ampullaris posterior tritt durch den hintersten, von einem kleinen Septum teilweise abgegrenzten Teil des Foramen acusticum inferius in das Cavum vestibulare durch und läuft dann durch den kurzen, oben (S. 331) beschriebenen Kanal in die Ampulla posterior ein.

Der Nervus facialis mit dem Nervus intermedius nehmen ihren Ursprung aus der Seitenfläche der Medulla oblongata gegenüber dem Foramen acusticum superius (Fig. 41), vereinigen sich und ziehen dicht über dem rostralen Ende des Ganglion vestibulare in den primären Facialiskanal ein. In dessen lateraler Mündung findet sich dorsal und rostral das Ganglion geniculi (Fig. 43), das rostralwärts den Nervus petrosus superfacialis major entsendet und sich in dieser Richtung an der Fovea geniculi entlang streckt. Der Hauptstamm des Nervus facialis passiert durch den ventrokaudalen Teil der lateralen Mündung des primären Facialiskanals, zieht sich ventralwärts biegend durch das Cavum supracochleare und tritt durch den sekundären Facialiskanal durch (Fig. 42). Aus der Apertura tympanica canalis facialis austretend läuft der Nerv dorsal von dem Stapes-Incusgelenk in dem Sulcus facialis kaudalwärts, tritt aber nicht in die Fossa muscularis minor (Fossa m. stapedii) ein, sondern biegt nach ventrokaudal um und zieht in dieser Richtung lateral von dem Stapes weiter zwischen Crista parotica und Musculus stapedius, passiert die Rinne an der kaudalen Fläche der Querspange des Stylohyale (s. unten S. 361), um schliesslich kaudolateral von dem Reichertschen Knorpel ventralwärts umzubiegen. An der letztgenannten Biegung findet die Verbindung mit dem Nervus auricularis vagii und wahrscheinlich mit dem oben beschriebenen lateralwärts ziehenden Glossopharyngeusast statt. Eben in der genannten Rinne wird die Chorda tympani abgegeben. Sie tritt in dem Winkel zwischen der Querspange und der Verbindungsspange des Stylohyale hervor, sucht sich unmittelbar zu der medialen Fläche des ersteren hin (Fig. 41) und folgt dieser

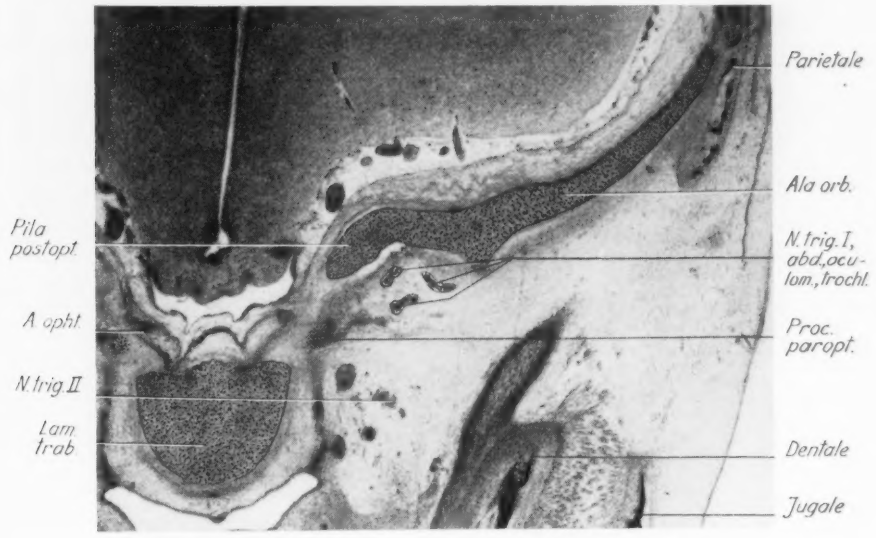

Fig. 52. Stad. XII. Schnitt durch Foramen opticum. 20/1.

rostralwärts, geht, der dorsalen Begrenzung der Trommelhöhle entlangziehend, ventrolateral an dem Stapes-Incusgelenk vorbei (Fig. 42) und passiert in unmittelbarer Nähe, und zwar medial von der Insertionsstelle des Musculus tensor tympani medial von dem Manubrium mallei (Fig. 43). Dann läuft sie weiter dorsalwärts und nach vorn in etwas kürzerem Abstand von der Schneckenkapsel als von dem Corpus mallei, zuerst medial und dann rostral von dem Tensor tympani (Fig. 44) und gelangt schliesslich an eine Stelle medial von dem Meckelschen Knorpel, dem sie sich in ihrem weiterem Verlauf allmählich nähert. Etwa auf der Höhe des vorderen Endes des Tegmen tympani bildet die Chorda tympani ein kleines, gut abgesetztes Ganglion (Fig. 45).Der Nervus petrosus superfacialis major zieht aus der Fovea geniculi vorwärts über die dorsolaterale Fläche der Schnekenkapsel von dem hinteren Teil des Ganglion semilunare überlagert hin (Fig. 44, 45), verlässt die Ohrenkapsel nahe deren vorderer Kuppel und nimmt den von dem Plexus caroticus kommenden Nervus petrosus profundus major auf unter Bildung eines kleinen Ganglion.

Nervus abducens verläuft in der Regio otica medial von der Schneckenkapsel und passiert dorsal von dieser weiter rostralwärts medial von dem vorderen Teil des Ganglion semilunare. Dieses Ganglion wird rostral von der Commissura suprafacialis von der rostralwärts ziehenden Wurzel des Nervus trigeminus gebildet. Es hat von der Seite gesehen die Form eines etwas langgesstreckten Vierecks breitet sich mit seinem hinteren Teil auf der laterodorsalen Fläche der Prominentia cochlearis superior aus (Fig. 44, 45) und streckt sich nach hinten bis an das Ganglion geniculi. Rostralwärts dehnt

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sich das Ganglion semilunare über die vordere Kuppel der Pars cochlearis hinaus.

*

Arteria carotis interna läuft, von zwei sympatischen Nerven begleitet der ventralen Fläche der Schneckenkapsel folgend, rostral- und etwas medialwärts (Fig. 45, 46), steigt in dem seichten Sulcus caroticus an der rostroventralen Fläche der Schneckenkapsel dorsalwärts (Fig. 46), passiert die Öffnung zwischen der Ala temporalis und der Lamina trabecularis und ist somit in das Cavum cranii gelangt.

Eine den Stapes durchziehende Arteria stapedialis fehlt dem vorliegenden Stadium. (Über Arterien vgl. weiter LINDAHL und LUNDBERG 1946.)

An der medialen Fläche der Seitenwand des Cavum cranii wird die Pars canicularis von dem Sinus sigmoideus umfasst. Dieser läuft zunächst dorsal von der Pars canalicularis der Fissura capsuloparietalis entlang (Fig. 39), biegt dann ventral um, folgt dem kaudalen Rand der Ohrenkapsel und dringt in den Sulcus sigmoideus ein, den er ganz ausfüllt, während er weiter vorn, den Nerven Platz machend, den lateralen Teil des tieferen Recessus jugularis einnimmt (Fig. 39), um schliesslich als Vena jugularis interna durch das Foramen jugulare auszutreten.

d. Regio orbitotemporalis.

1. *Als Ganzes.*

Die Orbitotemporalregion setzt sich aus der Lamina trabecularis, die vorn in ein kurzes Septum interorbitale übergeht, den Alae temporales und den Alae orbitales zusammen. Charakteristisch ist die schwache Verbindung mit der Oticalregion, sowie die unvollständige Ausbildung des Bodens des Cavum epiptericum und der Seitenwand des Cavum cranii. Sowohl eine Commissura alicochlearis wie eine Commissura orbitoparietalis fehlen.

2. *Lamina trabecularis.*

Als Fortsetzung des Planum basale streckt sich die Lamina trabecularis nach vorn, den medianen Teil des Bodens der Orbitotemporalregion ausmachend. Ihr ventraler Rand stellt annähernd eine Gerade dar, die mit dem Planum basale einen stumpfen Winkel von etwa 155° bildet (Fig. 37). Die Grenze zwischen der Lamina trabecularis und dem Planum basale erscheint auf der ventralen Fläche als eine Abknickung, macht sich auf der cerebralen Fläche dagegen als eine quergestellte Leiste, die Crista transversa, bemerkbar, die das rostrale Ende der Parachordalplatte ausmacht

und demgemäss eigentlich der Oticalregion zugerechnet werden sollte. Die Crista transversa ist von einer medianen Einsenkung in zwei laterale Höcker aufgeteilt (Fig. 36), die den Pfeilern eines reduzierten Dorsum selle entsprechen dürften. Die Höhe der Trabekelplatte ist hier fast gleich deren doppelter Breite. Rostral wird die Lamina trabecularis allmählich breiter und gleichzeitig hiermit senkt sich ihre cerebrale Fläche und bildet eine flache Mulde, die Fossa hypophyseos oder Sella turcica, deren Mitte sich trichterförmig zur Bildung des Canalis hypophyseos vertieft (Fig. 36, 37, 49, 50). Während die Begrenzung des Querschnittes der Trabekelplatte hinten die Form einer halben dorsoventral gestreckten Elipse hat, deren gerade Kante der subcerebralen Fläche entspricht, nähert sie sich mit rostralwärts zunehmender Breite immer mehr einem Halbkreis. Der kaudalen Hälfte der Fossa hypophyseos fehlen Seitenwände (Fig. 37). Vorn verbreitern sich dagegen die Ränder der Lamina trabecularis nach lateral und dorsal und bilden die flachen Processus alares (Fig. 35—37, 49, 50), die sich in rostrokaudaler Richtung von kurz hinter dem Canalis hypophyseos bis zu einer Stelle gegenüber der Mitte dieses Kanals ausdehnen. An den Processus alaris schliesst sich lateral die Ala temporalis an. In dem Winkel zwischen dieser und der rostrolateralen Kante der Fossa hypophyseos fügt sich die Cartilago pilae postopticae ein, die sich mit der genannten Kante und dorsolateral mit der hinteren Wurzel der Ala orbitalis homokontinuierlich verbindet (Fig. 37). Dieser Knorpel bildet folglich den Ansatzteil der hinteren Orbitalwurzel. Er hat seine grösste Ausdehnung in rostromedialer Richtung, ist durch Furchen sowohl an der lateralen wie an der medialen Fläche von Orbitalflügel und Trabekelplatte gut abzugrenzen und schickt einen kleinen Fortsatz als Processus paropticus rostrolateralwärts in das Foramen opticum hinein (Fig. 34—37, 52). Der genannte Forsatz dient als Ansatzstelle der Musculi recti des Augenbulbus. — Die umfangreiche Hypophyse füllt immer noch den Canalis hypophyseos aus und streckt sich, ohne die Ränder der Trabekelplatte wesentlich zu überragen, von der dorsalen Mündung des Kanals bis zu der Crista transversalis. Der rostrale Teil der Fossa hypophyseos wird von Bindegewebe ausgefüllt.

Der vordere Abschnitt der Trabekelplatte, die Pars chiasmatica, streckt sich mit abnehmender Breite und zunehmender Höhe rostralwärts und geht schliesslich ohne Grenze in das sehr kurze Septum interorbitale über. Der Querschnitt ist unmittelbar vor der Fossa hypophyseos, wo sich die cerebrale Fläche ventralwärts senkt und die flache Fovea hypochiasmatica bildet, wieder etwas seitlich zusammengedrückt mit etwas geringerer Höhe als Breite. Rostralwärts nimmt er allmählich immer mehr dreieckige Form an, indem die seitlichen Flächen ebener und die ventrale schmäler werden (Fig. 53 d).

Die Fovea hypochiasmatica (Fig. 35, 37) ist durch einen breiten, niedrigen, quergestellten Wulst, Tuberculum sellae, mit dem

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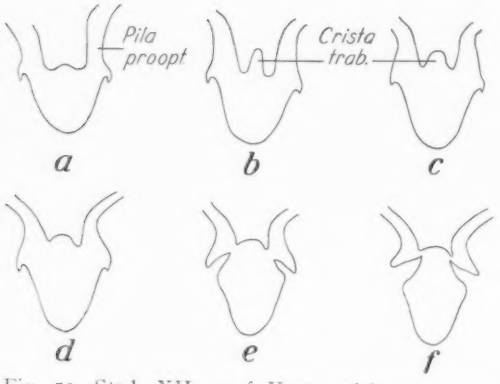

Fig. 53. Stad. XII. *a—f* Konturzeichnungen von Schnitten durch den vorderen Teil der Lamina trabecularis von hinten nach vorn geordnet. 10/1.

höchsten Punkt zwischen den Wurzeln der Processus paroptici von der Fossa hypophyseos getrennt. Sie bedingt eine Vergrösserung des Foramen opticum, nimmt aber nicht das Chiasma in sich auf, sondern ist mit Bindegewebe ausgefüllt. Entlang der cerebralen Fläche der Pars chiasmatica zieht eine mediane, niedrige Leiste, die Crista trabecularis (Fig. 36). Diese hat nahe an ihrem an der rostrodorsalen Fläche des Tuberculum sellae gelegenen hinteren Ende einen viereckigen Querschnitt, der nach vorn abgerundet wird und schliesslich ein breites, niedriges Dreieck darstellt. In der vorderen Hälfte der Fovea hypochiasmatica wird die Basis des Dreiecks allmählich kürzer (Fig. 53 a), und die Crista erhebt sich zwischen den vorderen Orbitalwurzeln zu einer etwas höheren, dünnen Lamelle (Fig. 53 b), die rostralwärts rasch an Stärke zunimmt (Fig. 53 c), sich zum Teil mit ihren lateralen Flächen mit den Pilae proopticae verbindet (Fig. 53 d—f) und rostral von diesen das kurze Septum interorbitale (Fig. 34, 54) bildet. Die Ränder der Fovea hypo-

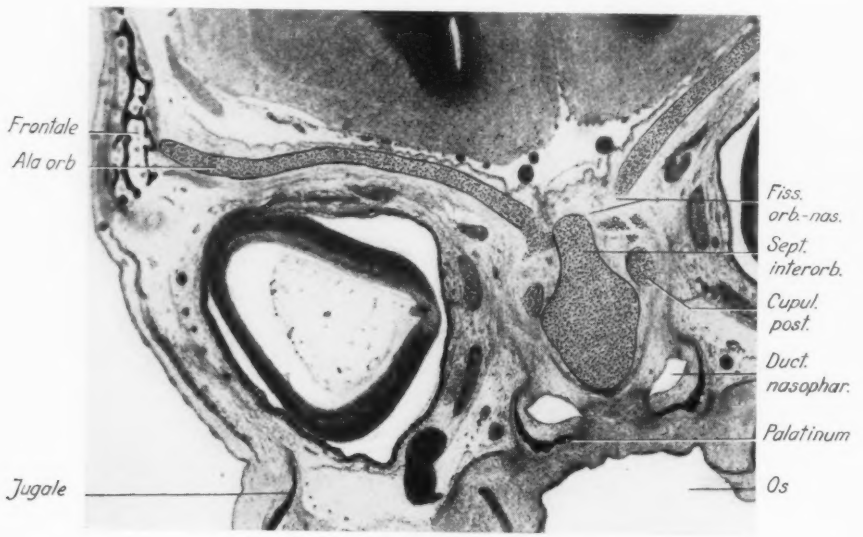

Fig. 54. Stad. XII. Schnitt durch Septum interorbitale. 20/1.

chiasmatica sind hinten eine kurze Strecke abgerundet, stehen aber weiter nach vorn mit scharfer Kante dorsolateralwärts hervor, um schliesslich im vorderen Teil der Fovea immer noch hervorstehend von je einer niedrigen, dünnen, paramedial verlaufenden und ventralwärts gerichteten Knorpelleiste begleitet zu werden. Diese zieht rostralwärts lateral von der Verlötung zwischen der vorderen Orbitalwurzel und der Trabekelplatte (Fig. 53 a—d). Über ihr Verhalten noch weiter rostralwärts s. Fig. 53 e—f.

3. *Ala orbitalis.*

Die wohl entwickelte Ala orbitalis besteht aus einer dünnen Knorpelplatte, die an drei Stellen an dem sonstigen Kranium befestigt ist, nämlich rostral an der lateralen Begrenzung der Fenestra olphactoria durch die Commissura sphenoethmoidalis und medial durch die beiden Orbitalwurzeln, Pilae prooptica und postoptica, an der Lamina trabecularis (Fig. 34—36). Wie oben angegeben fehlt eine Commissura orbitoparietalis. Zwischen der Commissura sphenoethmoidalis und der Pila prooptica wird die Ala orbitalis von der Nasenkapsel durch die Fissura orbitonasalis getrennt, während die beiden Pilae das Foramen opticum umgreifen. Die Grundform des Orbitalflügels lässt sich am einfachsten auf ein rechtwinkliges Dreieck zurückführen (Fig. 34). Wir unterscheiden somit eine rostromediale Begrenzungslinie, die sich quer über die Commissura sphenoethmoidalis und entlang der Fissura orbitonasalis bis zu der vorderen Orbitalwurzel streckt, eine kaudomediale, die senkrecht auf der eben angeführten und von der vorderen Orbitalwurzel durch die Basis der hinteren kaudolateralwärts verläuft und schliesslich eine laterorostrale, die von dem hinteren spitzen Ende des Flügels in lateralwärts ausladendem Bogen rostromedialwärts bis zu dem vorderen Ende der Commissura sphenoetmoidalis zieht. Von der mediorostralen Begrenzungslinie steigt die Knorpellamelle dorsolateral auf, krümmt sich aber in dem Teil des Orbitalflügels, der kaudal von der Commissura sphenoethmoidalis folgt, bald nach lateral, um nochmals in der Nähe des lateralen Randes etwas nach dorsal umzubiegen. Ein Querschnitt zeigt folglich in dem betreffenden Teil flache S-Form (Fig. 54). Hinter der Pila prooptica ebnet sich die mediale der oben beschriebenen Biegungen aus, während der laterale Teil der Knorpelplatte sich nach dorsal krümmt (Fig. 52). Kaudal von der Pila postoptica wird die Ala orbitalis nur von diesem lateralen Teil, der sich zu einer ebenen, dorsolateral stehenden Platte ausrichtet, (Fig. 49, 50) nach hinten fortgesetzt. Der Form nach könnte es sich bei dem kaudalwärts ausgezogenen Ende des Orbitalflügels um einen Rest der Commissura orbitoparietalis handeln.

Die sehr kurze Commissura sphenoethmoidalis zeigt eine

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Breite von etwa derselben Länge wie die enge, bindegewebig geschlossene Fissura orbitonasalis, die in ihrem rostralen Gebiet den Nervus ethmoidalis aus der Orbita in das Cavum cranii durchlässt. Eine hier durchziehende Arteria ethmoidalis habe ich nicht auffinden können. Die Pila prooptica ist wenig von dem Flügel abgesetzt und trifft hinten von dorsal, vorn von dorsolateral und sogar von lateral auf die Lamina trabecularis. Ihr hinterer Teil verbindet sich mit dem lateralen Gebiet der leicht konkaven cerebralen Fläche der Lamina trabecularis und bildet lateral eine Crista (Fig. 53 a), deren Kante von einer ventralwärts herabhängenden, dünnen Knorpellamelle begleitet wird, die sich kaudalwärts weiter längs des Randes der Trabekelplatte fortsetzt (siehe oben S. 338). Nach vorn rückt der mediale Teil der Pila immer mehr auf der lateralen Fläche der Crista trabecularis hinauf, sodass diese beiden Gebilde sich scheinbar entlang einer laterodorsalwärts blickenden Fläche verbinden (Fig. 53 b—d). Von dieser Fläche löst sich weiter nach vorn das verbreiterte Ende der Pila in der Weise ab, dass ihre lateroventrale Kante die Fortsetzung der vorher erwähnten lateralen Crista bildet, während ihre mediodorsale Kante die Verbindung mit der Crista trabecularis beibehält (Fig. 53 e). Die von diesen beiden Kanten begrenzte Fläche der Pila dreht sich dann allmählich, sodass sie in ihrem vordersten Teil schliesslich ventral blickt (Fig. 53 f). Die lange, gegen ihr mediales Ende an Breite abnehmende, von der Ala orbitalis gut abgesetzte Pila postoptica geht von der kaudomedialen Begrenzungslinie ersterer etwas dorsalwärts ab, biegt bei gleichzeitiger Drehung gegen die Medianebene medioventral um und verschmilzt homokontinuierlich mit der Cartilago pilae postopticae (Fig. 51). An der Stelle, wo die Ala orbitalis in die Pila postoptica übergeht, findet sich an der ventralen Fläche eine Crista (Fig. 52), die die freie laterokaudal ziehende Kante des Flügels über die Basis der Pila fortsetzt. An der dorsalen Fläche macht sich eine Eindellung an der entsprechenden Stelle bemerkbar.

4. *Ala temporalis.*

Die Ala temporalis stellt eine etwa gleichseitig dreieckige Knorpelplatte dar, deren cerebrale nach dorsal leicht konkave Fläche in einer frontalen Ebene liegt (Fig. 34, 36). Die eine Seite streckt sich leicht rostralwärts gebogen senkrecht zur Lamina trabecularis, die gegenüberliegende Spitze folglich kaudalwärts. Von den zwei übrigen Spitzen ist die eine abgerundet und lateralwärts gerichtet, während die zweite sich medial streckt und sich mit dem Processus alaris und der Cartilago pilae postopticae homokontinuierlich verbindet (Fig. 35, 36). Eine Commissura alicochlearis ist nicht vorhanden.

Der Temporalflügel setzt sich zusammen aus einer lateralen Lamina ascendens, einer medialen kaudal gerichteten Spina alaris, einer

von diesen beiden rostroventral ausgehenden Lamina pterygoidea und schliesslich einem Zwischenstück, das den medialen Teil der vorderen freien Kante des Flügels in Anspruch nimmt und rostral sonst in die Cartilago pilae postopticae, medial in den Processus alaris, kaudal in die Spina alaris und lateral in die Lamina ascendens übergeht. Die kleine Lamina ascendens stellt eine Platte dar, die sich vorn etwas dorsalwärts aufrichtet (Fig. 34, 36, 37). Sie kommt hierdurch der ventralen Kante des hinteren Abschnittes der Ala orbitalis nahe, jedoch ohne diese zu berühren. Durch eine grosse Einbuchtung, die Incisura ovalis, in der laterokaudalen Begrenzungslinie des Flügels und durch die rostralwärts gerichtete Biegung dessen vorderen Randes erhält die Lamina ascendens ovale Form. (Fig. 55). Sie ist von einem grossen, runden Foramen rotundum durchbrochen, das rostroventral blickt und durch das der Nervus maxillaris das Cavum epiptericum verlässt (Fig. 43, 50). Kaudomedial geht die Lamina ascendens in ein breites kaudalwärts auslaufendes, stachelähnliches Gebilde über (Fig. 34, 36, 55), das von TERRY bei der Katze als „a prominent spine" beschrieben wird, und das ich als Spina alaris bezeichne. Von dem hinteren Teil der Lamina ascendens und dem lateralen vorderen Teil der Spina alaris geht die etwas rostralwärts gebogene dreieckige Lamina pterygoidea ventralwärts ab, die in ihrem dorsalen Teil sehr dick, ventralwärts aber dünner ist (Fig. 34, 36, 55). Sie wird von einer tief einschneidenden, senkrecht auf der Lamina ascendens stehenden Spalte in einen längeren Processus pterygoideus medialis und einen kürzeren Processus pterygoidus lateralis aufgeteilt. Die Arteria maxillaris interna tritt durch diese Spalte hindurch, die folglich einem Foramen alisphenoideum (Canalis alaris) entspricht, und die ich somit als Fissura alisphenoidea bezeichne. — Die Ala temporalis bildet den Boden des Cavum epiptericum. Ein selbstständiger Pterygoidknorpel ist noch nicht vorhanden. Auch habe ich keine s. g. Restknorpel auffinden können.

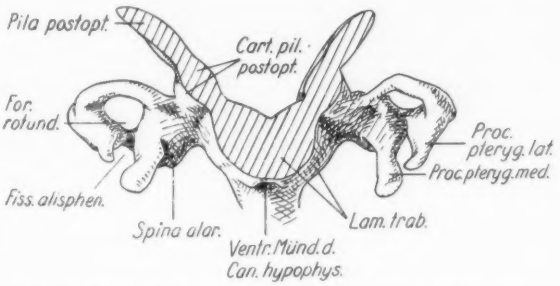

Fig. 55. Stad. XII. Der hintere Teil der Lamina trabecularis mit Alae temporales von rostroventral gezeichnet. 15/1.

5. *Nerven und Blutgefässe der Regio orbitotemporalis.*

Das Ganglion semilunare streckt sich gerade mit seinem rostralen Ende in die Region dorsal von der Spina alaris hinein, von der es ziemlich weit ent-

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fernt liegt. Der Nervus mandibularis geht von der ventralen Fläche des Ganglion semilunare aus und zwar in einiger Entfernung von dessen vorderem Ende, zieht lateral von dem hintersten Teil der Spina alaris ventralwärts und passiert also nicht durch die Incisura ovalis. Der Nervus maxillaris, der stärkste Zweig des Trigeminus, verlässt die rostroventrale Ecke des Ganglion, verläuft rostralwärts und etwas ventralwärts, zieht über den hinteren Rand der Lamina ascendens (Fig. 49) und tritt durch das Foramen rotundum aus dem Cavum cranii aus (Fig. 50), während der Nervus ophtalmicus etwa von der Mitte der vorderen Fläche des Ganglion semilunare ausgeht, dorsal von dem Nervus maxillaris nach vorn zieht (Fig. 49—51) und die Schädelhöhle verlässt, indem er sich dicht unter dem Bogen der Pila postoptica hält (Fig. 52).

Der Nervus abducens zieht medial von dem Ganglion semilunare rostralwärts, biegt etwas nach lateral, streicht lateral von der Arteria carotis interna und dorsal von dem vorderen Teil der Spina alaris, nähert sich dem Nervus ophtalmicus von medial und tritt zusammen mit diesem in die Orbita.

Der Nervus trochlearis läuft dorsal, der Nervus oculomotorius dorsomedial von dem Ganglion semilunare (Fig. 46). Rostral von diesem folgen sie in derselben Anordnung dem Nervus ophtalmcius, mit dem sie gemeinsam das Cavum cranii verlassen (Fig. 49—52).

Der Nervus vidianus (N. petrosus superficialis major et profundus major) zieht medioventral von der Spina alaris (Fig. 49), medial von der Lamina pterygoideus und ventral von dem Processus alaris (Fig. 50) rostralwärts zu dem Ganglion sphenopalatinum, das ventral von der Cartilago pilae postopticae und dorsolateral von dem Ductus nasopharyngeus liegt.

*

Über die Arteria carotis interna ist schon berichtet worden, dass sie rostral von der Gehörkapsel zwischen der Lamina trabecularis und der Spina alaris in das Cavum cranii tritt. Sie verläuft dann rostrolateralwärts und gibt dorsal von dem Processus alaris die Arteria ophtalmica ab (Fig. 49, 50). Diese macht einen medialen Bogen um die Pila postoptica, an deren mediale Fläche sie sich dicht anschmiegt (Fig. 51) und tritt durch den vorderen Teil des Foramen opticum aus dem Cavum cranii in die Orbita über.

Die Arteria maxillaris interna verläuft auf ihrem Weg rostralwärts medial von dem Nervus mandibularis und durch die Fissura alisphenoideum hindurch (Fig. 49, 50), wonach sie unmittelbar einen Ramus orbitalis abgibt (Fig. 51). (Über Arterien vgl. weiter LINDAHL und LUNDBERG 1946.)

e. Regio ethmoidalis.

1. *Als Ganzes.*

Die Ethmoidalregion wird von der Nasenkapsel gebildet, die in bekannter Weise durch ein medianes Septum in zwei Räume getrennt wird. Diese verlängern sich hier schlauchförmig rostralwärts von der vorderen Kante des Septum. Die Nasenkapsel nimmt etwa zwei Fünftel des Schädels in Anspruch und zeigt kurz hinter ihrer Mitte sowohl grösste Höhe wie Breite (Fig. 34, 35). Bis auf den vordersten etwas mehr als ein Fünftel der Kapsel umfassenden Teil, der sich im Verhältnis zu dem nach hinten folgenden Abschnitt etwas dorsalwärts aufrichtet, beschreibt die Nasenkapsel in ungebrochener Fortsetzung der Orbitotemporalregion einen nach ventral konkaven, weichen Bogen mit der grössten Biegung in der vorderen Hälfte des Septum nasi (Fig. 37).

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Zwei Hauptteile lassen sich an der Nasenkapsel unterscheiden, von denen der eine die hintere, der andere die vordere Hälfte umfasst: 1) Die hintere von dem Cavum cerebri überlagerte und von der sich nach vorn wenig aufrichtenden Lamina cribrosa überdachte Pars subcerebralis, 2) die vordere von dem nach vorn abfallenden Teil des Tectum nasi bedeckte Pars praecerebralis.

In dem Tectum findet sich als einzige Öffnung das Foramen epiphaniale. Auch die Seitenwand, Paries nasi, ist auffallend vollständig und zeigt bis auf die Fenestra narina keine Perforationen. Bemerkenswert ist aber, dass sich der ventrale Rand des Paries nasi in der Pars praecerebralis bedeutend weniger weit ventralwärts als das Septum nasi streckt, sodass hier dem epithelialen Nasensack eine knorpelige Bedeckung seitlich fehlt. Das Solum ist in für Säugetiere typischer Weise unvollständig. Es wird vorn von der breiten Lamina transversalis anterior, in der Mitte von der Cartilago paraseptalis, hinten von der Lamina transversalis posterior gebildet: letztere geht kaudalwärts in die hinten abschliessende Cupula posterior über, während die Nasenkapsel nach vorn weniger vollständig von einer Cupula anterior geschlossen wird.

Mit anderen Teilen des Chondrocranium verbindet sich die Nasenkapsel an drei Stellen, nämlich median durch das Septum nasi mit dem Interorbitalseptum und an den beiden Seiten durch die Commissura orbitoethmoidalis mit den Orbitalflügeln. Eine Verbindung zwischen der Cupula nasi und irgendwelchen Teilen der Regio orbitotemporalis fehlt (Fig. 34—36).

Im Gegensatz zu den schon beschriebenen Regionen besteht die Nasenkapsel an mehreren Stellen aus vorknorpeligem Gewebe, das oft in Blastem übergeht.

2. *Septum nasi.*

Sieht man von dem sehr kurzen Septum interorbitale ab, so bildet das Septum nasi eine unmittelbare Fortsetzung der Lamina trabecularis und ist folglich hinten in derselben Weise ausgebildet wie der vordere Teil der Trabekelplatte: Ventral ein breiter, im Querschnitt dreieckiger Knorpelstab mit abgerundeter ventraler Kante, dorsal eine dicke, medial stehende, von dem ven-

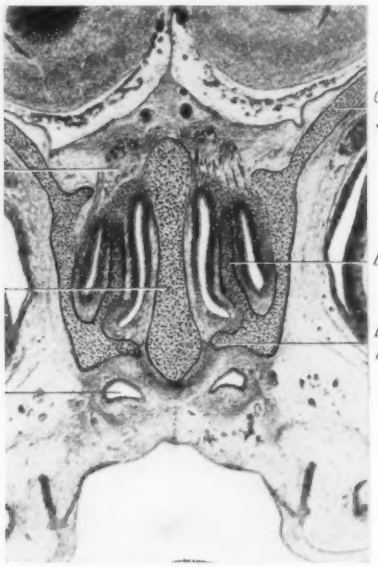

Fig. 56. Stad. XII. Schnitt durch Ethmoturbinale II. 20/1.

tralen Teil wenig scharf abgesetzte Platte, die rostrale Fortsetzung der Crista trabecularis. Nach vorn verliert die ventrale Verdickung schnell sowohl an Höhe wie an Stärke und hat schon am vorderen Rand der Lamina transversalis posterior den Charakter eines ventral abschliessenden Randwulstes der gleichzeitig rostralwärts höher und dünner werdenden Platte. Im hinteren Teil buchtet sich die laterale Fläche des Septum unmittelbar dorsal von dessen ventraler Verdickung zu einer grossen, sehr flachen Eindellung ein, die sich so weit nach vorn streckt wie die Lamina transversalis posterior (Fig. 56). Der ventrale Septumrand verläuft in dem subcerebralen Teil der Kapsel mit sehr kleiner Krümmung, die aber in dem praecerebralen zunimmt. Der dorsale Septumrand steigt innerhalb der Pars subcerebralis nach vorn etwas dorsalwärts an und ist hierbei mehr gebogen als das entsprechende Stück des ventralen Randes. Am Übergang in den praecerebralen Teil biegt er stärker ventralwärts um und fällt nach vorn ventralwärts mehr ab, als er im hinteren Teil gestiegen ist. Das

Septum erhält hierdurch ein Maximum an Höhe an der Grenze zwischen den beiden Hauptteilen der Nasenregion und ist rostral niedriger als kaudal von diesem Maximum (Fig. 37). Ein kurzes Stück des dorsalen Septumrandes zwischen den hintersten Enden der Cupulae posteriores ist frei. Rostral hiervon verschmelzen die Cupulae mit ihm, die kleine nach dorsal konvexe Lamina infracribrosa bildend (Fig. 34, 36). Der zwischen den beiden Fenestrae olfactoriae gelegene Teil des dorsalen Septumrandes ist teilweise mit den Spangen der Lamina cribrosa verbunden und an solchen Stellen verdickt.

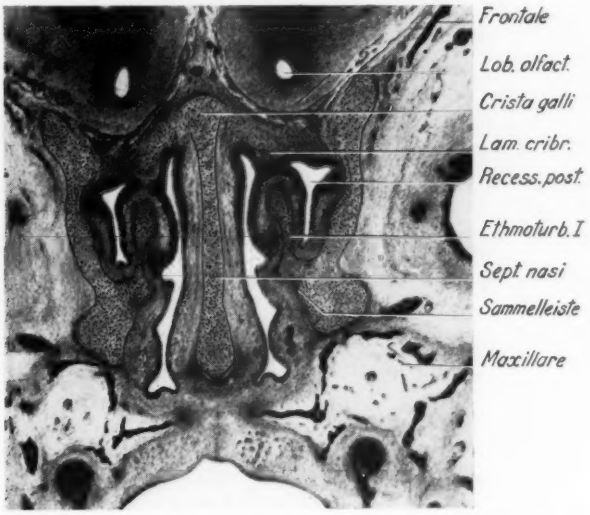

Fig. 57. Stad. XII. Schnitt durch Ethmoturbinale I. 20/1.

Zwischen den Anhaftungsstellen zweier Spangen endet er frei. Sein vorderster Teil dehnt sich aber stempelförmig mit einer dorsal ebenen Fläche seitlich aus (Fig. 59). Über den dorsalen Septumrand erhebt sich ein dicker, kaudodorsalwärts gerichteter, stumpfer Knorpelzapfen, die Spina mesethmoidalis, die eben auf der Grenze zwischen dem subcerebralen und dem praecerebralen Teil der Kapsel von dem Septum ausgeht (Fig. 34, 36, 37). Sie zeigt eine flache, rostrodorsal blickende Vorderfläche, an deren beiden lateralen Kanten die Cristae praecribrosae ein Stück fortsetzen. Von der dorsalen, hier breiten Fläche des Septumrandes wird ihr hinterer Teil durch eine dünne, bindegewebige Schicht getrennt. Eine niedrige Crista galli ist nur in der hinteren Hälfte der Lamina cribrosa vorhanden, von deren Balken sie sich wenig absetzt (Fig. 57). — Kaudal in dem praecerebralen Teil der Nasenkapsel zeigt der dorsale Septumrand T-Form, indem das

Tectum nasi hier von dem verdickten Rand sofort lateralwärts abgeht. Rostral findet sich dagegen ein sehr seichter Sulcus supraseptalis, der sich kurz vor dem vorderen Ende des Septums stark vertieft und sich nach hinten von dieser Stelle halbwegs zu der Crista mesethmoidalis streckt. Das Tectum geht hier mit zunehmender Tiefe des Sulcus immer mehr in dorsaler Richtung von dem Septumrand ab. Dem vordersten Teil der Pars praecerebralis fehlt das Septum, das zwischen den beiden rostralen Verlängerungen der Nasenkapsel mit dorsoventral stehender abgerundeter Kante aufhört (Fig. 37). An dieser ist eine kleine, von Bindegewebe geschlossene Lücke vorhanden, die die beiden Nasenhöhlen miteinander verbindet und auch eine Öffnung nach aussen herstellt. Die laterale, abgerundete Kante des hinten noch stark aufgetriebenen ventralen Teiles des Septum ist von dem ihm dicht anliegenden medialen Rand der Lamina transversalis posterior durch eine dünne Bindegewebsmembran getrennt (Fig. 56). Der ventrale Rand des Septum streckt sich dann frei und leicht verdickt nach vorn (Fig. 57—59) bis kurz hinter die Lamina transversalis anterior, wo er mit dem vorderen Drittel der Cartilago paraseptalis verschmilzt. Der hintere Teil dieses Knorpels schmiegt sich dem ventralen Septumrand dicht an, ohne sich mit ihm zu verbinden.

Die Lamina transversalis anterior geht von dem ventralen Septumrand ventrolateral aus. Es findet sich folglich hier ein Sulcus infraseptalis (Fig. 35), der sich rostralwärts vor der Lamina transversalis anterior schnell vertieft und sich vor dem vorderen Ende des Septum mit dem Sulcus supraseptalis vereinigt. Im vorderen Abschnitt der Lamina transversalis anterior wird dieser Sulcus aber von der Basis eines kleinen rostroventralwärts gerichteten, etwas nach dorsal gebogenen Knorpelstabes, Cartilago papillae palatinae, ausgefüllt (Fig. 35).

3. *Tectum nasi.*

Das Tectum nasi wird in dem subcerebralen Teil der Nasenkapsel von der immer noch ziemlich unvollständigen Lamina cribrosa gebildet (Fig. 35, 61). Diese schliesst die Fenestra olfactoria ab, liegt aber in einer etwas mehr ventralwärts gelegenen Ebene (Fig. 57—59). Die Fenestra olfactoria und somit auch die Lamina cribrosa zeigt die Form eines stumpfwinkligen Dreiecks, in dem das Septum nasi die längste Seite bildet (Fig. 36). Von den zwei übrigen Seiten, die sich nur wenig an Länge unterscheiden, streckt sich die kürzere mediorostral, die längere kaudomedial von dem stumpfen, dem Septum gegenüberliegenden Winkel. Die rostrolaterale Begrenzung der Fenestra olfactoria besteht medial aus der schon erwähnten Crista praecribrosa, die zu dem Tectum des praecerebralen Abschnittes gehört, lateral aus einem langgestreckten Buckel, Prominentia paracribrosa, der sich verschmälernd kaudalwärts in die Commissura

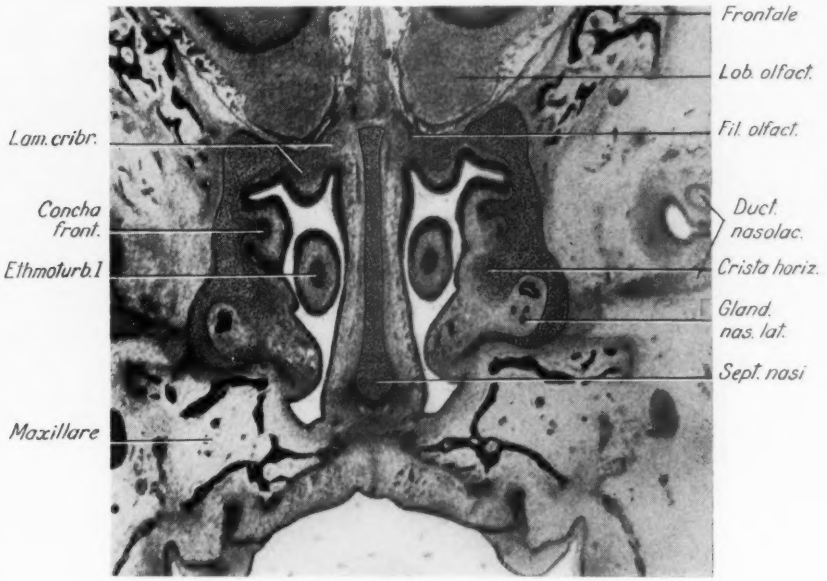

Fig. 58. Stad. XII. Schnitt durch Recessus lateralis. 20/1.

orbitoethmoidalis übergeht und rostromedial durch einen kleinen Einschnitt in dem Rand der Fenestra olfactoria, die Incisura praecribrosa, von der genannten Crista getrennt wird. Laterokaudal wird die Fenestra olfactoria hinten von der Paries nasi begrenzt, die die Fissura orbitonasalis nach vorn abschliesst, und in deren Bereich sie allmählich medial umbiegt. Die Seitenwand erreicht hinter der Fenestra olfactoria den dorsalen Septumrand, mit dem sie verschmilzt, die schon oben genannte Lamina infracribrosa bildend. Weiter nach vorn biegt sie fast rechtwinklig um und steht im hinteren Gebiet der Commissura orbitoethmoidalis als kleine, medial gerichtete Knorpelplatte, Limbus paracribrosus, hervor, von der die Crista intercribrosa rostromedialwärts abgeht. Im vorderen Gebiet der Commissura sphenoethmoidalis und medial von der Prominentia paracribrosa ist diese Knorpellamelle viel schmäler und richtet sich mit ihrer cerebralen Fläche als Fortsetzung der Commissura orbitoethmoidalis medioventralwärts.

Da der Dorsalrand des Septum nasi sich bedeutend über die lateralen Ränder der Fenestra olfactoria hebt, liegt die Lamina cribrosa nicht in einer Ebene, sondern zeigt eine nach dorsal hin konvexe Fläche (Fig. 57—59). Die noch nicht ganz vollständige Crista intercribrosa teilt die Lamina cribrosa in einen medial-hinteren und einen lateral-vorderen Abschnitt (Fig. 36). Die Foramina cribrosa des ersteren öffnen sich hauptsächlich in den Recessus posterior und lassen die Filae olfactoriae für dessen Riechschleimhaut durch, während durch die des letzteren die Filae olfactoriae für die Riechschleim-

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haut des Recessus lateralis treten. Das vorderste, immer noch ziemlich grosse Foramen cribrosum, in dessen rostrolaterale Begrenzung die Incisura praecribrosa einschneidet, lässt den Nervus ethmoidalis in die Nasenhöhle durch und schliesst folglich das Foramen cribroethmoidale in sich ein. Ein von kaudomedial auf die Incisura praecribrosa hinwachsender Knorpelstab teilt dieses Foramen auf. Das Tectum der Pars praecerebralis streckt sich im hinteren Gebiet, wo die Nasenkapsel stark seitlich ausladet, weiter lateralwärts als in dem vorderen. Die stellenweise leicht anzugebende Grenze folgt einer seichten Furche, die der Insertionslinie des Nasoturbinale an der inneren Fläche der Nasenkapsel entspricht. Diese Furche fängt hinten an der Incisura praecribrosa an, streckt sich rostralwärts bis zu dem dorsalen Ende des Sulcus lateralis anterior, zieht ventral von dem Foramen epiphaniale, verliert sich rostralwärts, um, weiter nach vorn wieder in Erscheinung tretend, sich dem Sulcus supraseptalis allmählich zu nähern und dorsal von der Lamina transversalis anterior aufzuhören (Fig. 34, 35). Der vorderste Teil des Tectum nasi bildet zusammen mit der medialen Seitenwand der Kapsel eine nach vorn teilweise abschliessende Cupula anterior (Fig. 35, 37). In dem hinteren Teile der Pars praecerebralis, wo ein Sulcus supraseptalis nicht vorhanden ist, bildet das Tectum eine grosse, einheitliche, aber niedrige Wölbung. Zwischen dieser einerseits und der Spina mesethmoidalis mit den Cristae praecribrosae andererseits findet sich eine flache Eindellung, von derem hinteren Rand das Tectum von zwei dicht zusammenstehenden feinen Kanälen durchsetzt wird, die kleine Arterien in die Nasenkapsel durchtreten lassen (Fig. 35).

4. *Paries nasi.*

Die Seitenwand der Nasenkapsel lässt drei nacheinander liegende Abschnitte unterscheiden. Der kaudale ist der kürzeste und wird von dem mittleren, auch hinsichtlich der Länge intermediären, durch eine seichte Furche, Sulcus lateralis posterior, abgegrenzt. Von dem mittleren Abschnitt wird der vordere, der den hinteren an Länge um das Doppelte übertrifft, durch eine scharfe Einknickung, den Sulcus lateralis anterior, getrennt (Fig. 34).

Der Sulcus lateralis posterior verläuft derart, dass das kaudale Viertel der Commissura sphenoethmoidalis sich mit dem hinteren, die rostralen drei Viertel der Commissura sich mit dem mittleren Abschnitt der Seitenwand verbinden. Sein dorsales Ende trifft damit auf die Commissur an einer Stelle, von der die Crista intercribrosa an der medialen Fläche abgeht. Der hintere Abschnitt der Seitenwand zeigt eine wenig modellierte laterale Fläche, die hinten in die Cupula posterior übergeht und in dem hinteren Gebiet der Fissura orbitonasalis, wie oben beschrieben, dorsalwärts allmählich gegen

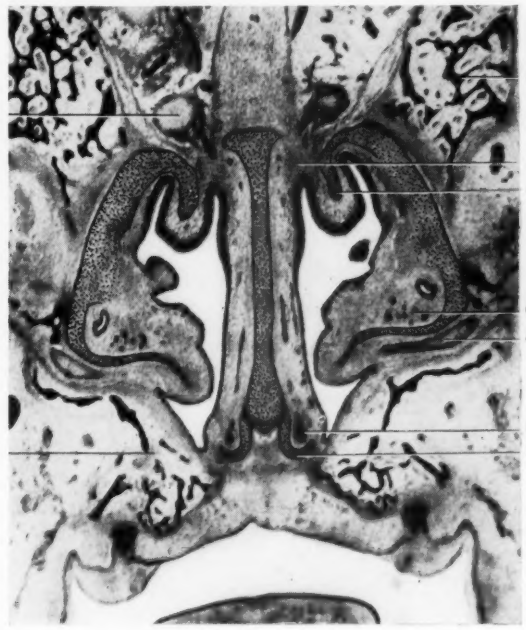

Fig. 59. Stad. XII. Schnitt durch das vorderste Foramen cribrosum. 20/1.

die Medianebene hin umbiegt, nach unten dagegen senkrecht gegen die Medianebene abgeknickt ist und hier eine schmale Lamina transversalis posterior bildet. Die vorderen zwei Fünftel des Abschnittes bilden eine paramedial stehende ebene Fläche, die sich dorsalwärts gegen die Fissura orbitonasalis mit einer von derem vorderem Ende kaudoventralwärts verlaufenden Kante absetzt (Fig. 34). Ventral knickt diese Fläche medial sehr scharf um, eine spitze Kante bildend. Der Sulcus lateralis posterior entspricht der Insertionslinie des Ethmoturbinale I im Inneren der Nasenkapsel.

Der mittlere Abschnitt der Seitenwand buchtet sich im vorderen Teil sehr stark lateralwärts hervor und bildet eine sich nach vorn und seitlich wölbende mächtige Kuppel, die neben dem schmäleren vorderen Abschnitt der Nasenkapsel hervorsteht. Diese Kuppel, die ventral breiter als dorsal ist, zeigt eine wenig gekrümmte, rostralwärts blickende Fläche, die ventral nach hinten umbiegt und den stark ausladenden Teil der Kapsel von ventral abschliesst. Die laterale Fläche der Kuppel ist verhältnismässig eben und geht unter starker Biegung in die rostrale und die ventrale über. Nach dorsal biegt sie vorn allmählich medial um und erreicht die zwischen Incisura praecribrosa und dem dorsalen Ende des Sulcus lateralis anterior ziehende Furche, geht aber hinten, bedeutend weniger gebogen, in die dorsalwärts vorspringende Prominentia paracribrosa über (Fig. 34, 36). Die

eben beschriebene Kuppel birgt den Recessus lateralis inferior anterior und den vorderen Teil des Recessus lateralis superior und wird als Prominentia anterior bezeichnet. Nach hinten steht der mittlere Abschnitt der Nasenkapselwand immer weniger lateralwärts hervor. Er grenzt sich hier durch eine ganz seichte Rinne von der Commissura sphenoethmoidalis ab und weist eine markante Furche, Sulcus horizontalis, auf, die hinten der ventralen Begrenzung der Seitenwand parallel entlangzieht und in einem nach vorn gerichteten Bogen dorsalwärts der Prominentia paracribrosa zustrebt (Fig. 34). Diese Furche dehnt sich nach hinten bis zu dem Sulcus lateralis posterior aus und kann nach vorn bis auf die Höhe des hinteren Endes der Cartilago paraseptalis verfolgt werden. Sie entspricht bis auf den hinteren kurzen longitudinal verlaufenden Teil der Insertionslinie der Crista horizontalis im Inneren der Nasenkapsel. Der Sulcus horizontalis unterteilt den mittleren Abschnitt des Paries nasi in eine dorsale, breite und niedrige und eine ventrale, schmale und hohe wulstförmige Prominenz. Erstere, die den hinteren Teil des Recessus lateralis superior einschliesst, wird als Prominentia superior bezeichnet und ist dorsal von der Grenzfurche gegen die Commissura sphenoethmoidalis, kaudal von dem Sulcus lateralis posterior, rostroventral von dem Sulcus horizontalis umgrenzt. Die vorderen Enden der eben genannten Grenzfurche und des Sulcus horizontalis nähern sich einander nach vorn, doch ohne sich zu vereinigen, und hier geht die Prominentia superior in die Prominentia anterior über (Fig. 34). Die von der Prominentia anterior kaudoventralwärts rostroventral von dem Sulcus horizontalis ziehende Prominenz wird grösstenteils von dem Recessus lateralis inferior posterior (Recessus maxillaris) durchzogen und wird folglich Prominentia posterior genannt. Ihr kaudalwärts umgebogener ventraler Teil ist hinten solide und stellt an dem ventralen Rand der Seitenwand eine kräftige Verdickung dar (Fig. 57), von der an der medialen Fläche sechs verschiedene Knorpellamellen ausstrahlen, nämlich der nach vorn ziehende ventrale Rand der Seitenwand, die Crista horizontalis, die beiden Lamellen des Ethmoturbinale I, und nach hinten ziehend, die Sammelleiste und die Seitenwand (Fig. 61). Diese Verdickung zeigt hinten an dem Sulcus lateralis posterior eine ventrale scharfe Kante, die nach vorn sich allmählich abrundet. Die rostroventrale Fläche der Prominentia posterior und der Prominentia anterior gehen mit einem stumpfen Winkel ineinander über. Medial biegt die erstgenannte Fläche ventralwärts um und bildet den dünnen, medioventralwärts gerichteten freien Rand der Seitenwand (Fig. 59). Hierdurch entsteht nahe an dem Rand eine flache, medioventralwärts offene Rinne, die den Ductus nasolacrymalis aufnimmt. Die freie Kante stellt den hinteren Teil des Maxilloturbinale dar und hört medioventral von der Prominentia posterior mit einem kaudoventral gerichteten, platten Fortsatz auf (Fig. 34, 35).

An dem vorderen Abschnitt des Paries nasi fällt, wie oben

hervorgehoben, auf, dass er sich in dem hinter der Lamina transversalis posterior gelegenen Gebiet viel weniger weit ventralwärts als das Septum ausdehnt. Der ventrale, von Knorpel nicht bedeckte Teil des epithelialen Nasensackes wird von dem Intermaxillare und dem Maxillare abgeschlossen. Der vordere Abschnitt des Paries nasi zeigt rostral von dem mittleren Teil des Sulcus lateralis anterior einen langgestreckten, im Inneren den Sulcus supraconchalis bergenden Wulst, Prominentia supraconchalis, der sich in der Richtung von dem Foramen epiphaniale zu der Lamina transversalis anterior streckt (Fig. 34). Zwischen ihr und dem hinteren Teil des Sulcus lateralis anterior findet sich eine ebene, dreieckige Fläche. Zu der breiten Lamina transversalis anterior, die in höherem Grade an der Bildung von Boden als von Seitenwand beteiligt ist, kommen wir unten zurück. Ihre Verbindung mit der Seitenwand besteht aus einem von ihrem vorderen Ende dorsomedial ausgehenden kurzen, schmalen und abgeflachten Knorpelstab, der die Fenestra narina von der Fenestra basalis trennt (Fig. 34). Der ventrale Rand der Seitenwand, der sich besonders ventral von der Prominentia supraconchalis hochzieht, ist von dem vorderen Teil der Prominentia anterior bis zu der Verbindungsspange der Lamina transversalis anterior medial eingebogen und bildet eine dünne, ventromedial gerichtete, leicht nach lateroventral konkave Knorpellamelle (Fig. 60), die Maxilloturbinale, die an Breite von hinten nach vorn abnimmt. Die Kante dieser Lamelle besteht aus jungem Knorpelgewebe und geht in eine dünne Blastemplatte, über. Der Ductus nasolacrymalis zieht der seichten Rinne der ventrolateralen Fläche der Maxilloturbinale entlang und passiert lateral von dem Verbindungsstab der Lamina transversalis anterior rostralwärts. Die sehr langgestreckte, hinten von der Lamina transversalis anterior begrenzte Fenestra narina blickt im vorderen Teil rostrolateralwärts, im hinteren lateralwärts (Fig. 35). Dies kommt dadurch zustande, dass das vordere Ende der Nasenkapsel nur medial nach vorn als Cupula anterior abgeschlossen ist, und dass ihre ventrale aus der medialen Nasenkapselwand bestehende Begrenzung weit lateralwärts hervor steht. Diese Wand biegt etwas rostral von der Mitte der Fenestra narina nach lateral und dorsal um und bildet einen breiten wenig abgesetzten Processus lateralis ventralis, der zusammen mit dem Processus alaris superior die Fenestra in eine kleine vordere und eine grössere hintere Öffnung teilt (Fig. 34, 35). Durch erstere zieht der Schleimhautsack der Nase seitlich nach aussen, um in die Haut überzugehen, durch letztere tritt der Ductus nasolacrymalis mit dem Schleimhautsack in Verbindung. Processus alaris superior, der ventral aus jungem Knorpel und Vorknorpel besteht, ist wie der Rand der Paries, von dem er ausgeht, aus Blastem aufgebaut. Nahe an dem vorderen Ende der Fenestra narina geht noch ein kleiner Processus alaris inferior lateralwärts von dem dorsalen Rand ab. Dieser

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ist unmittelbar vor der Lamina transversalis anterior und dem Processus alaris superior dorsalwärts eingekrempelt und bildet kleine Atrioturbinalia (Fig. 61).

5. *Solum nasi.*

Die beiden Laminae transversales und die Cartilago paraseptalis stellen den Boden der Nasenkapsel dar. Von diesen gehen die Lamina transversalis und der Paraseptalknorpel von dem Septum aus, während die Lamina transversalis posterior von der Paries nasi aus gebildet wird. Ein grosser Teil des Bodens wird von der Fenestra basalis eingenommen, die mit wechselnder Breite sich von dem vorderen Ende der Cupula posterior bis zu der Verbindungsspange der Lamina transversalis anterior streckt (Fig. 35).

Die Lamina transversalis posterior stellt den Boden in dem hinteren Abschnitt der Nasenkapsel dar. Sie ist eine Fortsetzung der Paries nasi, der unter etwa rechtwinkliger Abknickung (Fig. 56) medial umbiegt und zeigt die Form eines gleichschenkligen Dreiecks mit dem einzigen spitzen Winkel nach hinten gerichtet (Fig. 35). Lamina transversalis posterior ist nach ventral leicht konkav und ihr medialer Rand, der der lateralen Kante der ventralen Verdickung des Septum folgt, ist von diesem durch eine enge, von Bindegewebe ausgefüllte Spalte getrennt (Fig. 56). Ihre rostrale Fortsetzung dreht sich mit dem medialen Rand dorsalwärts. Gleichzeitig hiermit nimmt sie an Breite ab und setzt sich weiter nach vorn als ganz schmale Leiste fort an der Innenseite des verdickten Teils der Prominentia posterior und in einigem Abstand von derem ventralen Rand (Fig. 61). Diese Leiste, die sich nur gegen dorsal abgrenzt, stellt die sogenannte Sammelleiste SEYDELS (1896) dar. Es fehlt folglich der Nasenkapsel jeglicher Boden unmittelbar vor der Lamina transversalis posterior, wo die Fenestra basalis auch ihre grösste Breite erreicht. Hinter der Lamina transversalis posterior treffen die mediale und die laterale Fläche der Cupula posterior in einer etwas abgerundeten Kante zusammen, die dorsalwärts zu der hinteren Spitze der Kapsel verläuft.

Die Cartilago paraseptalis besteht aus zwei, einer medialen höheren und einer lateralen niedrigeren, ventral zu einer Rinne vereinigten Knorpellamellen. Erstere öffnet sich folglich nach dorsolateral (Fig. 59). Die paramedial stehende mediale Lamelle ist zu einem Drittel ihrer Länge mit der lateralen Kante des ventralen Septumrandes verschmolzen und zwar an einer Stelle, die sich ventral von der Prominentia supraconchalis befindet. Von hier aus streckt sie sich nach hinten dem verdickten Septumrand von der Seite angeschmiegt und hört ventral von der Prominentia posterior auf (Fig. 34, 35). Eine Verbindung mit der Lamina transversalis posterior fehlt also. Rostralwärts geht die mediale Lamelle dorsal in die Lamina transversalis anterior über, ventral setzt sie sich in die immer noch sehr kurze Cartilago

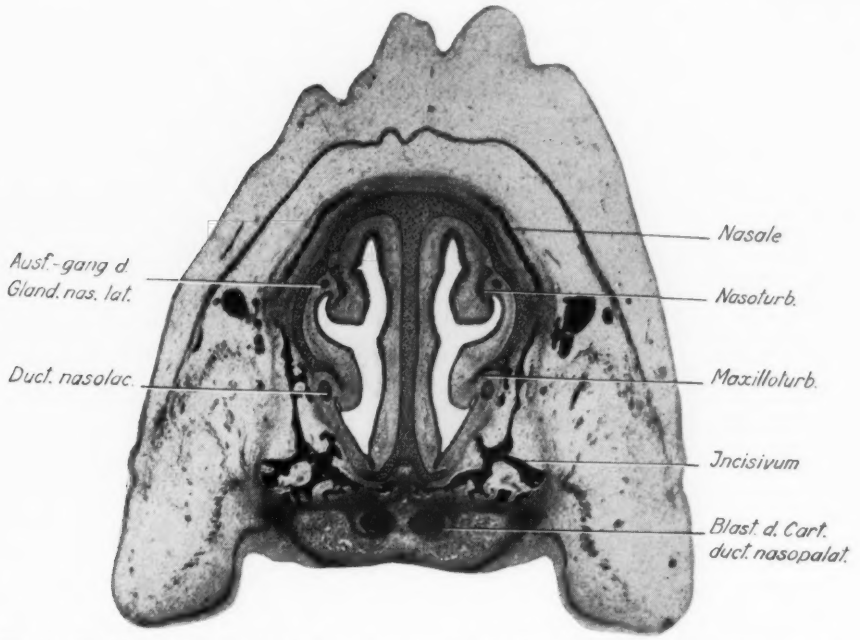

Fig. 60. Stad. XII. Schnitt durch den vorderen Teil der Lamina transversalis anterior. 20/1.

ductus nasopalatini fort. An diesem läuft die Rinne des Paraseptalknorpels rostralwärts weiter, allerdings nach der Seite hin offen, da die laterale Lamelle des Paraseptalknorpels sich hier lateralwärts richtet (Fig. 34). Der vordere Teil der Cartilago ductus nasopalatini ist weitgehend als Blastem angelegt. Dieses streckt sich rostralwärts als geschlossene Röhre, die sich bald medioventralwärts (Fig. 60), weiter nach vorn ventralwärts in Form einer Rinne öffnet. Die nach hinten geschlossene Rinne des Paraseptalknorpels enthält das Jacobsonsche Organ, das sich durch die Rinne des Nasopalatinknorpels mit ganz dünnem Hals in das oben beschriebene blastematische Rohr fortsetzt. Hier mündet es in den lateral von dem Jacobsonschen Organ in das Rohr eindringenden Ductus nasopalatinus, der aus dem rinnenförmigen vorderen Teil des Blastems ventralwärts umbiegt und in die Mundhöhle mündet. Von vorn drängen sich zwei flache, paramedial stehende knöcherne Fortsätze, die Processus palatini der Intermaxillaria, zwischen die Paraseptalknorpel ein, die an ihrem vorderen Rand etwas lateralwärts gebogen sind.

Die breite Lamina transversalis anterior ist in ihrer ganzen Ausdehnung mit dem ventralen Septumrand verbunden. Von diesem geht sie lateralwärts und mehr oder weniger ventralwärts ab, biegt aber bald dorsal um, sodass sich ihr grösster Teil nach dorsolateral hin erstreckt. Ihr hinterer schmälerer Teil (Fig. 34, 60) setzt sich in die mediale Lamelle des Para-

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septalknorpels fort. Weiter nach vorn, wo die Lamina ihre grösste Breite hat, läuft ihr Rand in kurzem Abstand von der ventralen Kante des Maxilloturbinale und zwar parallel mit dieser. Von dem vordersten Teil dieses Randes geht die schmale Knorpelspange aus, die die Lamina transversalis anterior mit dem Paries nasi verbindet (Fig. 34). Die vordere, die Fenestra narina begrenzende Kante der Lamina geht rostralwärts in die laterale Kante der medialen Nasenkapselwand über. Auch diese trägt im Gebiet des Processus lateralis ventralis zur Bildung des Bodens der Nasenkapsel bei.

6. *Binnenraum.*

Die übliche Einteilung der Innenfläche des Paries nasi in drei Abschnitte, eine Pars posterior s. ethmoturbinalis, eine Pars anterior s. maxillonasoturbinalis und ein zwischen diesen beiden nach der Seite vorgebuchteter Recessus lateralis, sind auch hier angebracht. Von diesem machen die Pars ethmoturbinalis und der Recessus lateralis zusammen die Pars subcerebralis aus, während die Pars maxillonasoturbinalis den praecerebralen Teil der Nasenkapsel darstellt.

Charakteristisch für die Pars ethmoturbinalis sind die Ethmoturbinalia, die sich medialwärts von der Seitenwand als dünne Knorpellamellen in den Binnenraum hineinstrecken und hier mit von hinten, dorsal und lateral nach vorn, ventral und medial parallel verlaufenden freien Rändern aufhören (Fig. 61). Die drei vorhandenen Ethmoturbinalia nehmen an Grösse von vorn nach hinten ab. Das Ethmoturbinale I inceriert entlang einer Linie an der Paries nasi, die dem Sulcus lateralis posterior an der Aussenfläche entspricht. Sein lateraler Teil inceriert dorsal an der Crista intercribrosa, während er ventral mit der beschriebenen kompakten Knorpelmasse der Prominentia posterior verschmilzt. In der Mitte ist die Verknorpelung schwächer gewesen, sodass hier eine von Blastem geschlossene Lücke zurückgeblieben ist. Die mediale leicht verdickte und etwas medial eingerollte Kante des Ethmoturbinale I verbindet sich dorsal mit der Lamina cribrosa an dem vorderen Ende der Crista intercribrosa. Ventral endigt sie frei und biegt scharf in eine nach ventral und hinten stehende Kante um, die sich mit der Sammelleiste und der ventralen, oben beschriebenen Wandverdickung verbindet (Fig. 61). An der Umknickungsstelle zieht sich die mediale Kante in einen rostrodorsal gerichteten Fortsatz aus. Kaudal von dieser Kante sitzt eine zweite, kürzere, medial und rostralwärts umgekrempelte Lamelle von medial und kaudal dem lateralen Teil des Ethmoturbinale I auf. Sie erreicht nicht die Lamina cribrosa, verbindet sich aber ventral in derselben Weise wie die Hauptlamelle des Ethmoturbinale I. Von der Medianebene aus gesehen (Fig. 61) bilden die beiden Lamellen, deren Kanten parallel gerichtet sind, zusammen eine Platte, die in ihrer Längsrichtung von einer breiten Rinne durchzogen

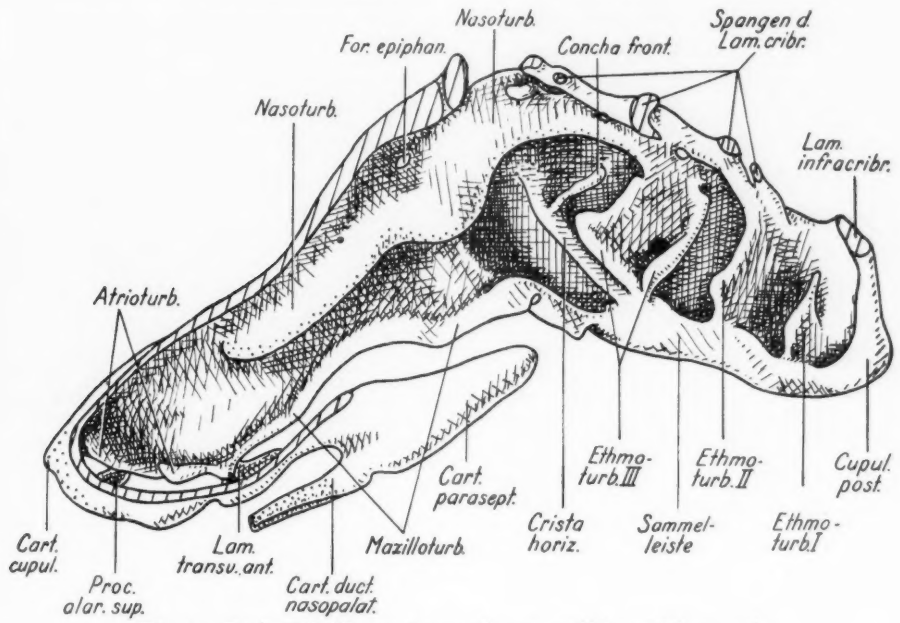

Fig. 61. Stad. XII. Nasenseitenwand von medial gezeichnet. 15/1.

ist. — Ethmoturbinale I trennt die Pars ethmoturbinalis von dem Recessus lateralis. Auch Ethmoturbinale II, das sich sowohl mit der Lamina cribrosa wie mit der Sammelleiste verbindet, zeigt einen Fortsatz, der allerdings kürzer und stumpfer ist und sich nach rostromedial richtet (Fig. 61). Das kleine Ethmoturbinale III erreicht bei weitem nicht den dorsalen Rand der Paries nasi. Ventral ist es mit der Lamina terminalis posterior verschmolzen. Zwischen Ethmoturbinale I und II ist an der Seitenwand eine breite, niedrige Erhebung vorhanden, die als Anlage eines Ektoturbinale aufzufassen ist. Der hinterste Teil der Region wird von einer kurzen, medialen Wand abgeschlossen. Diese ist medial leicht konvex und passt in die entsprechende seichte Eindellung an dem Septum hinein. Auch zwischen Ethmoturbinale I und II ist eine mediale Wand vorhanden, obwohl sehr niedrig. Sie wird von der Sammelleiste gebildet, die sich in etwa unveränderter Richtung als Crista horizontalis in den Recessus lateralis fortsetzt.

Die Pars maxillonasoturbinalis ist durch die Anwesenheit des Maxilloturbinale und des Nasoturbinale charakterisiert. Durch das Fehlen einer Crista semicircularis grenzt sie sich nicht sehr scharf von dem Recessus lateralis ab (Fig. 61). Über die zwei kleinen Atrioturbinalia ist schon oben berichtet worden, wie auch über das Maxilloturbinale. Es sei hier nur nochmals genannt, dass sich das letztere von der Verbindungsspange der Lamina transversalis anterior bis zum hinteren Teil der Prominentia anterior

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streckt, und dass es, wie auch beim erwachsenen Tier, nicht nach dorsal umgekrempelt ist. Dorsal von dem Maxilloturbinale verläuft das Nasoturbinale in der Längsrichtung der Nasenkapsel. Es besteht aus einer hohen, dünnen Knorpellamelle, die sich nach vorn bis dorsal von der Mitte der Lamina transversalis anterior streckt. Nach hinten zieht es unmittelbar lateral von dem Foramen epiphaniale auf die Incisura praecribrosa zu, folgt dem medialen Rand der Prominentia paracribrosa und geht hinter dieser in die Lamina cribrosa über (Fig. 61). Nach vorn setzt es sich in Form eines Blastems ein Stück weiter fort. Von Interesse ist, dass dieses Blastem selbständig angelegt wird und erst sekundär sich mit dem Paries nasi verbindet. Auch der Abschnitt unmittelbar hinter dem Foramen epiphaniale besteht immer noch hauptsächlich aus Vorknorpel. Im übrigen ist die Kante des ganzen Maxilloturbinale vorknorpelig und blastematisch. Im grossen und ganzen hängt es der Medianebene parallel herunter; nur an einigen Stellen, vor und hinter dem Foramen epiphaniale, zeigt sein ventraler Rand eine Tendenz, lateralwärts auszuweichen, offenbar ein Anfang zu der später einsetzenden Umkrempelung in dieser Richtung. An einer Stelle, die dem Foramen epiphaniale näher liegt als dem vorderen Ende des Maxilloturbinale, wird dieses auf einer kurzen Strecke durch ein kleines Loch von dem Paries nasi getrennt (Fig. 60, 61). Durch dieses Loch tritt eine kleine, in der Längsrichtung der Nase ziehende Arterie von der medialen zu der lateralen Seite des Maxilloturbinale hindurch. In dem Winkel zwischen dem Nasoturbinale und dem Tectum nasi zieht der Ramus lateralis des Nervus ethmoidalis von dem Foramen cribroethmoidale rostralwärts. An dem Foramen epiphaniale angelangt, teilt er sich in zwei Zweige, von denen der eine die Nasenhöhle durch das genannte Foramen verlässt, der andere sich weiter verästelnd nach vorn fortsetzt. In dem Winkel zwischen dem Nasoturbinale und dem Paries nasi zieht der Ausführungsgang der Glandula nasalis lateralis rostralvärts (Fig. 60), um in den epithelialen Nasensack kurz hinter dem Processus alaris superior einzumünden. Ventral von der vorderen Hälfte des Nasoturbinale und dorsal von dem Maxilloturbinale ist eine seitliche Ausbuchtung, Sulcus supraconchalis, der Paries nasi vorhanden.

Der Recessus lateralis wölbt sich in Übereinstimmung mit der äusseren Form der Paries nasi viel stärker vorn als hinten lateralwärts hervor. Medial ist er durch eine grosse Öffnung zugänglich (Fig. 61). Als Fortsetzung der oben beschriebenen Sammelleiste zieht eine kräftige, hohe, der Seitenwand entspringende Knorpellamelle, die Crista horizontalis, von dem ventromedialen Ende des Ethmoturbinale I rostrodorsalwärts durch den Recessus lateralis. Die Knorpellamelle inceriert entlang einer Linie, die dem Sulcus horizontalis an der Aussenfläche des Paries entspricht und wird von einem niedrigen, flachen, medial blastematischen Wulst fortgesetzt. Dieser trifft in der Mitte zwischen dem Foramen epiphaniale und der Incisura

praecribrosa auf den Teil des Nasoturbinale, der dem oberen Schenkel der Crista semicirculare entspricht. Hierdurch wird der Recessus unvollständig in einen dorsalen Abschnitt, Recessus lateralis superior (s. Recessus frontalis) und einen ventralen Abschnitt, Recessus lateralis inferior aufgeteilt (Fig. 61). Der Recessus lateralis superior dessen kaudaler Teil von dem Ethmoturbinale I medial abgeschlossen wird, ist wiederum durch eine senkrecht zu der Crista horizontalis von der Seitenwand einspringende Lamelle, Concha frontalis (Concha obtectae) aufgeteilt (Fig. 61). Diese ist vorknorpelig bis blastematisch und erreicht dorsal nicht die Lamina cribrosa, während sie sich ventral mit der Crista horizontalis verbindet. Der dorsal-vordere Teil des Recessus lateralis superior, der sich bis in die Prominentia paracribrosa erstreckt, wird von dem hintersten Teil des Nasoturbinale medial abgedeckt (Fig. 59). Der Recessus lateralis inferior bildet an sich einen einheitlichen Raum, an dem wir eine schlauchförmige, niedrige Ausstülpung, den Recessus lateralis inferior posterior (s. Recessus maxillaris), von einem weiteren vorderen Teil, dem Recessus lateralis inferior anterior, unterscheiden können. In dem letztgenannten finden sich rostrolateral und ventrolateral die verzweigten Kanäle der Glandula nasalis lateralis (Fig. 59), die von hier aus tief in den Recessus lateralis inferior posterior eindringen (Fig. 58). Der Ausführungsgang dieser Drüse fängt in dem rostrodorsalen, von dem Nasoturbinale medial abgeschlossenen Teil des Recessus lateralis inferior anterior an.

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f. Visceralskelett.

Der Meckelsche Knorpel stellt einen rundlichen Knorpelstab dar, der sich homokontinuierlich mit dem Malleus verbindet (Fig. 34, 36, 62). Von diesem streckt er sich zunächst über ein knappes Siebentel seiner Länge gerade nach vorn bis auf die Höhe der Spina alaris, beschreibt dann einen grossen, weichen, nach ventral konvexen Bogen, der etwa 5/7 seiner Länge umfasst und gelangt hierbei wieder auf die Verlängerung des kaudalen geraden Stückes. Hierauf folgt eine Abknickung ventralwärts, sodass der rostrale, etwas mehr als 1/7 der Gesamtlänge ausmachende Teil dieselbe Hauptrichtung zeigt, wie der absteigende Abschnitt des grossen Bogens. Das abgeknickte Stück, dessen rostrale Hälfte die Symphyse bildet, richtet sich wiederum an der etwas verdickten Spitze dorsalwärts auf. Diese stellt einen unpaarigen, kurzen Fortsatz dar (Fig. 62). Gleich kaudal von der Abknickungsstelle ist der Meckelsche Knorpel in einem kleinen Gebiet vollkommen aufgelöst (Fig. 34, 62). Hier sind die ersten Anzeichen einer enchondralen Ossifikation vorhanden, die später zur Bildung eines in dem Os dentale ganz eingeschlossenen Os mentomandibulare führt. Ein weniger weit fortgeschrittener Knorpelabbau findet sich in geringer Ausdehnung sowohl kaudal wie rostral von dem Ort des voll-

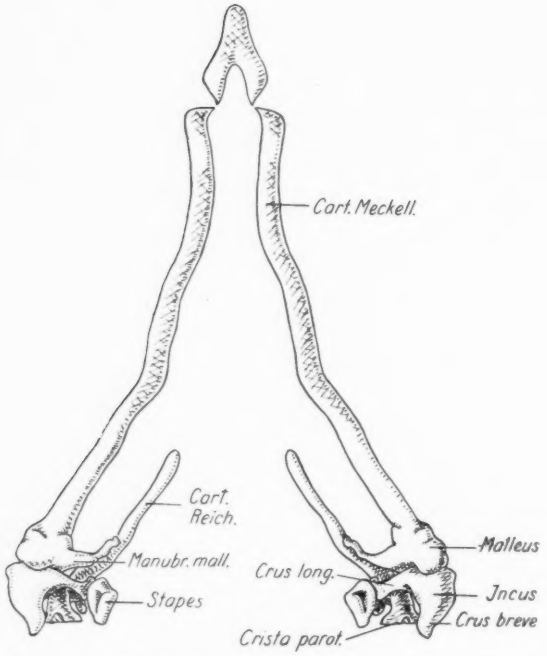

Fig. 62. Stad. XII. Projektion des Visceralskelettes von dorsal. 10/1.

ständigen Abbaues. In diesem ganzen Gebiet ist der Meckelsche Knorpel mehr oder weniger vollständig von einer periostalen Knochenlamelle umgeben, die mit den Lamellen des Os dentale zusammenhängt. In der Nähe des Malleus nimmt der Querschnitt des Meckelschen Knorpels ovale Form an mit der längeren Achse von laterodorsal nach medioventral verlaufend.

Kaudalwärts setzt sich der Meckelsche Knorpel in dem von der Seite zusammangedrückten Malleus fort, dessen hinterer sich nach ventrokaudal hin fortsetzender Abschnitt die gegen den Incus articulierende Gelenkfläche trägt (Fig. 34, 35, 62, 63). Dieser Abschnitt setzt sich in das schlanke Manubrium mallei fort, dessen Hauptrichtung medioventral ist. Sein proximalstes Stück hält diese Richtung ein. Durch eine hierauf folgende Biegung erhält der nächste Abschnitt mediale Richtung, während das Endstück medioventral und etwas nach vorn gerichtet ist (Fig. 34, 62). Nahe an der genannten Biegung des Manubrium mallei findet sich ventral ein Processus lateralis und kaudal ein ganz kleiner Processus muscularis, die Insertionsstelle der Sehne des Musculus tensor tympani (Fig. 63). Das Manubrium mit dem Processus lateralis liegt in der bindegewebigen Anlage des Trommelfelles eingeschlossen (Fig. 44). In dem vorderen Abschnitt des Capitulum ist die Längsachse des Querschnittes wie in dem hinteren Teil des Meckelschen Knorpels stark lateralwärts geneigt.

Die ventrorostralwärts blickende, sattelförmige Gelenkfläche der Incus schliesst das Corpus incudis nach vorn ab. Dieses setzt sich nach hinten in das lange, sehr kräftige Crus breve fort, das einen sich verjüngenden Knorpelstab mit ovalem Querschnitt darstellt (Fig. 63). Crus breve streckt sich kaudalwärts entlang der Crista parotica und dringt mit seiner Spitze in die Fossa incudis ein (Fig. 34, 35), wo es durch zwei dünne Ligamente mit der Ohrenkapsel verbunden ist. Das sich verjüngende Crus longum geht von einer Stelle

in der Nähe der rostralen Fläche des Corpus aus und streckt sich medioventralwärts, biegt nahe seinem Ende medial um und bildet eine schmale, in der Längsrichtung des Schädels ausgezogene Kante aus, die mit dem Stapes articuliert (Fig. 35, 62, 63).

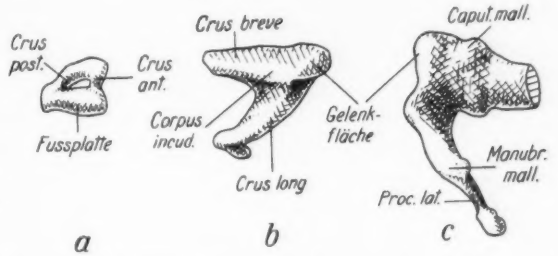

Fig. 63. Stad. XII. *a* Stapes; *b* Incus und *c* Malleus der linken Seite, alle mit dem rostralen Ende nach rechts gezeichnet. 15/1.

Durch die flache Form der hinteren Fläche des Malleus und der vorderen der Incus bilden das Capitulum mallei und das Corpus incudis eine geschlossene Einheit, die durch eine feine Spalte von dem Gewölbe des Tegmen tympani (in weiteren Sinne) getrennt wird. Auch kommen hierdurch Manubrium mallei und Crus longum incudis dicht nebeneinander zu liegen. Zwischen den Gelenkflächen des Malleus-Incus-gelenkes und des Incus-Stapes-gelenkes findet sich ein dichtes, embryonales Füllgewebe.

Der Stapes hat seine definitive Form erreicht. Seine stark in die Länge gezogenen Fussplatte fügt sich, von dichtem Bindegewebe umgeben, in die Fenestra ovalis ein. Sie besteht aus einem, in die beiden Crura übergehenden Kern aus voll ausgebildetem Knorpel und einer äusseren, hiervon scharf abgesetzten Schicht aus jungem Knorpel, die den Kern rings herum in der Ebene der Fenestra ovalis und von medial umgibt (Fig. 41). Von den beiden Crura stapedis ist das vordere Crus anterius (s. rectilineum) gerade und kürzer als das hintere gebogene Crus posterius (s. curvilineum Fig. 63). Wie oben angegeben findet sich in dem vorliegenden Stadium keine Arteria stapedialis.

Von dem Hyobranchialskelett gehe ich nur auf den proximalen Teil des Hyalknorpels oder Reichertschen Knorpels ein. Wie oben angegeben verbindet sich dieser homokontinuierlich von vorn mit dem ventralen Teil der Crista parotica und streckt sich von hier aus zunächst in der Hauptsache ventrokaudal. Dieser Teil, an dem wir drei verschiedene Abschnitte unterscheiden können, und der mit dem folgenden durch ein sehr kurzes Ligament verbunden ist (Fig. 41), ist als Stylohyale zu bezeichnen. Die drei Abschnitte des Stylohyale zeichnen sich durch verschiedene Verlaufsrichtung und Stärke aus und werden am besten durch Fig. 47 veranschaulicht. Das mit der Crista parotica verschmolzene Laterohyale ist kurz und grob, mit einer vorderen konvexen und einer hinteren ebenen Fläche versehen und streckt sich als Querspange von lateral, dorsal und rostral nach medial, ventral und kaudal. Der folgende Abschnitt, die Verbindungsspange, ist sehr kurz und dünn, geht von dem kaudalsten Teil des Endes der Querspange aus und behält zwar etwa dieselbe

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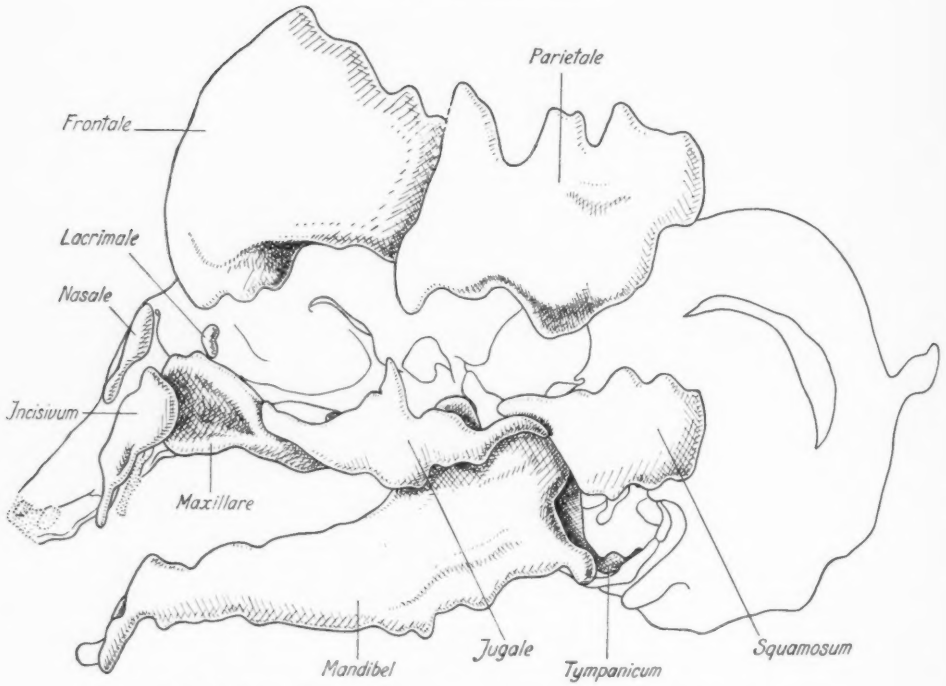

Fig. 64. Stad. XII. Deckknochen. Projektion von der Seite. 10/1.

Richtung wie diese bei, aber mit stärkerer Betonung von „ventral und kaudal" als „medial" (Fig. 34). Der dritte Abschnitt, die Ventralspange, ist wiederum grob und länger und streckt sich kaudoventralwärts. Seine vordere, ebene Fläche ist mit dem dorsalen Ende an der Verbindungsspange befestigt, während die hintere Fläche nach hinten konvex ist. Diese Verhältnisse bedingen,

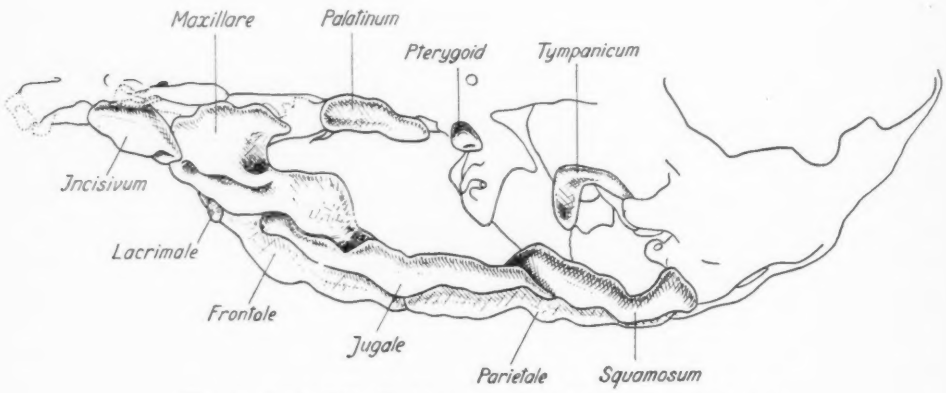

Fig. 65. Stad. XII. Deckknochen. Projektion von ventral. 10/1.

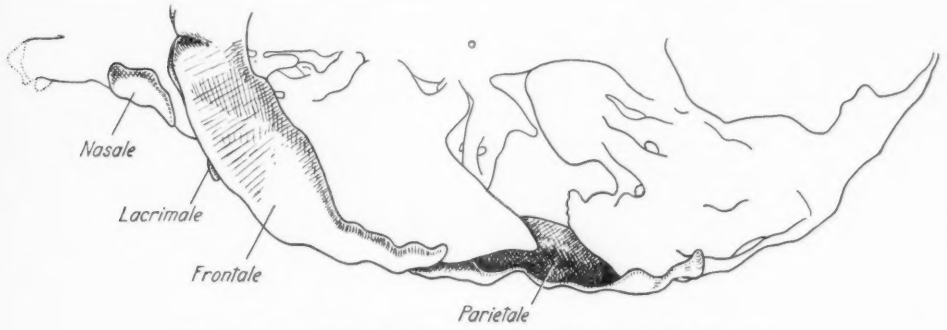

Fig. 66. Stad. XII. Deckknochen. Projektion von dorsal. 10/1.

dass die Ventralspange sich weiter kaudal als die Querspange befindet, wodurch der Zwischenraum zwischen ersterer und dem benachbarten Teil der Crista parotica als eine an der Hinterseite der Querspange verlaufende kaudalwärts offene Rinne erscheint, durch die der Nervus facialis zieht.

Der durch das kurze Ligament mit dem Stylohyale verbundene, einheitliche Teil des Reichertschen Knorpels, das „Epihyale", zieht zunächst ventralwärts bis zu dem Niveau des vorderen Randes des Foramen perilymphaticum und biegt dann nach vorn und medial um (Fig. 34, 62).

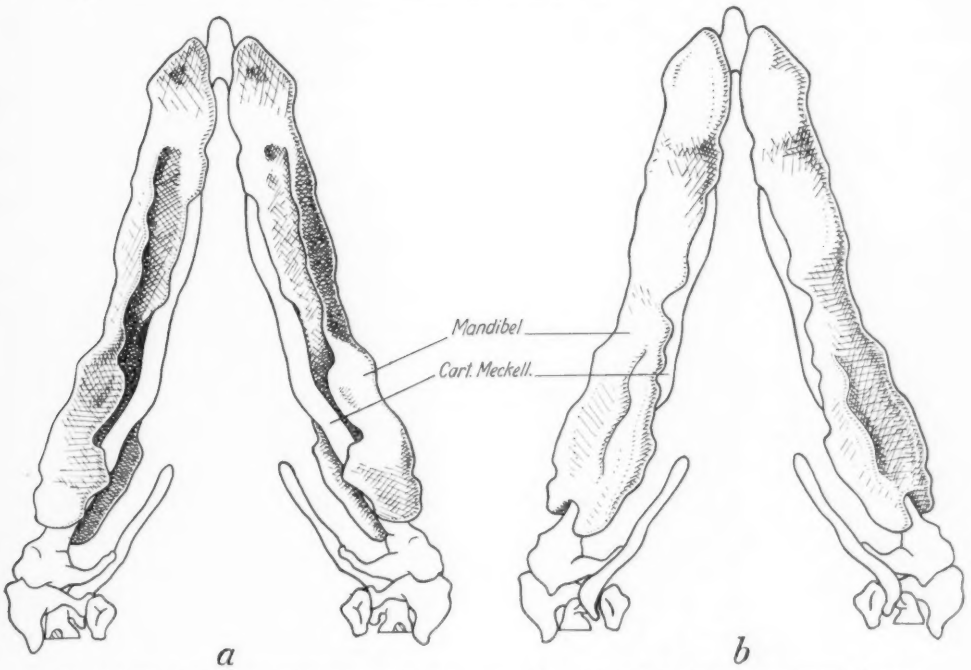

Fig. 67. Stad. XII. Unterkiefer mit Meckelschem Knorpel. *a* Projektion von dorsal; *b* von ventral. 10/1.

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g. Deckknochen.

Zu den in Stadium XI schon angelegten Deckknochen, Dentale Squamosum, Jugale, Maxillare, Frontale, Parietale und Lacrimale haben sich noch Incisivum, Palatinum und eine Pterygoidkomponente hinzu gefügt.

ÜBER EINIGE SPÄT AUFTRETENDE KNORPELDIFFERENZIERUNGEN.

STADIUM XIII—XIV: SCHEITEL-STEISS-LÄNGE 36 UND 42 MM, KOPFLÄNGE 16,5 UND 20 MM, FIG. 68—69.

Obwohl das Stadium XII als „Stadium optimum" betrachtet wird, treten in der folgenden Entwicklung noch einige Knorpeldifferenzierungen auf und zwar in der Orbitotemporal- und in der Ethmoidalregion. In letzterer erfolgt die Verknorpelung der Blasteme der Lamina cribrosa und der Turbinalia und Cartilago ductus nasopotatini erreicht allmählich seine endgültige Form. In voll ausgebildetem Zustand ist dieser Knorpel von BROOM (1898, 1909) eingehend beschrieben worden und wird deswegen hier nicht berücksichtigt.

Die Veränderungen in der Orbitotemporalregion werden an Hand von Stadium XIII und XIV beschrieben. In dem erstgenannten findet der Verschluss des Canalis hypophyseos gerade statt, und zwar dadurch, dass eine hohe sagittale Knorpellamelle, die von der vorderen Wand des Kanales nach hinten wächst, den Kanal ausfüllt. Diese Knorpellamelle ist als Intertrabekel aufgefasst worden (vgl. LINDAHL 1946). Die Spitzen des Processus pterygoideus lateralis und des Processus pterygoideus medialis haben sich mit einander vereinigt, sodass hier eine Lamina pterygoidea vorliegt. Hierdurch ist die Fissura alisphenoidea in ein Foramen alisphenoideum verwandelt worden. Die ventrale Kante der Lamina pterygoidea verknöchert und auch längs der ganzen kaudalen Kante der Alae temporales hat Verknöcherung stattgefunden. Hierdurch ist die typiche Form der Spina alaris verschwunden. Der ziemlich grosse Pterygoidknorpel ist von einem dünnen Belag von Knochengewebe eingeschlossen.

In dem Stadium XIV haben die Alae temporales besonders stark an Grösse zugenommen und zeigen bis auf ein kleines Gebiet an der Lamina pterygoidea eine knöcherne Oberfläche. Die Verknöcherung hat auch auf den zwischen den Alae temporales gelegenen Teil der Trabekelplatte übergegriffen. Der canalis hypophyseos ist verschlossen, ohne dass Reste einer sagittalen Knorpellamelle wie in Stadium XIII beobachtet werden können. Zwischen dem jetzt stark verbreiterten Processus alaris und der rostralen Fläche der Pars cochlearis ist an jeder Seite ein kleines Knorpelstück vorhanden (Fig. 69, x) auf der Höhe der dorsalen Fläche des Planum basale und rostrolateral von der in das Cavum

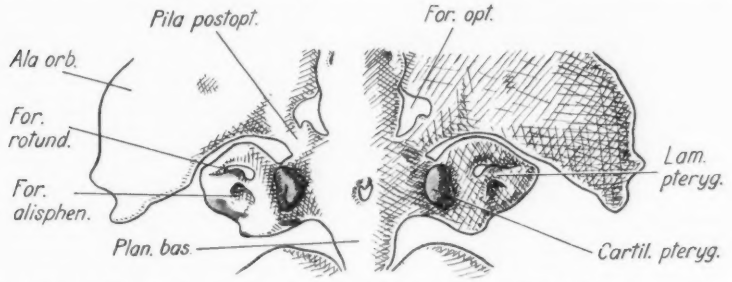

Fig. 68. Stad. XIII. Mittlerer Teil des Chondrocraniums. Projektion von ventral. 10/1.

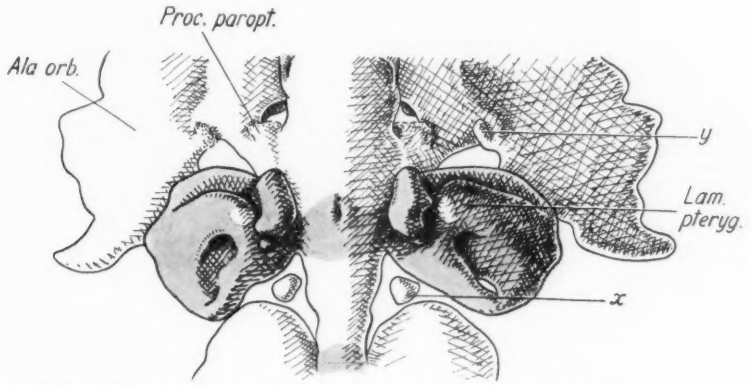

Fig. 69. Stad. XIV. Mittlerer Teil des Chondrocraniums. Projektion von ventral. 10/1.

cranii eintretenden Carotis interna. Das späte Auftreten dieses isolierten Elementes legt den Gedanken nahe, es handele sich um einen s. g. Restknorpel. Hiergegen spricht aber die Tatsache, dass es gerade den Platz einnimmt, der für eine Commissura alicochlearis typisch ist, wohingegen die in dieser Region aufgefundenen Restknorpel eine bedeutend dorsalere Lage haben (vgl. z. B. MEAD 1909, VOIT 1909, MATTHES 1921). Es ist folglich eher als Rest einer reduzierten Commissura alicochlearis aufzufassen. Auch weiter rostrad ist ein kleines Knorpelelement aufgetreten und zwar an der ventralen Fläche der Ala orbitalis am kaudalen Rand letzterer (Fig. 69, y). An der linken Seite findet sich hier ein kleiner, schlanker mediorostrad gerichteter Knorpelstab. An der rechten Seite hat dasselbe Element immer noch Blastemcharakter und ist im Zusammenhang damit plumper. Die morphologische Bedeutung dieses Elementes wird in der Diskussion (S. 370) besprochen.

DISKUSSION.

Auf Grund äusserer Verhältnisse bin ich nicht in der Lage, die in dem deskriptiven Teil gewonnenen Tatsachen in wünschenswerter Ausführlichkeit

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und unter Berücksichtigung der sehr umfangreichen Literatur theoretisch zu behandeln. Die hier folgende kurze Diskussion sucht nur die Aufmerksamkeit auf die mehr auffallenden Ergebnisse zu lenken und berücksichtigt die Literatur äusserst knapp. Hinsichtlich anderer, hier nicht zitierter Arbeiten verweise ich auf die grossen Zusammenstellungen von MATTHES (1921—22), STADTMÜLLER (1936) und DE BEER (1937).

Beim Vergleich der Stadien IV bis XII fällt sofort auf, dass die Hauptbiegung der Schädelbasis eine regelmässige Verschiebung von hinten nach vorn erfährt. Sie liegt im Stadium IV—V auf der Grenze zwischen Basalplatte und Hypophysenplatte, in Stadium VI—VII in der Hypophysenplatte, in Stadium VIII auf der Höhe der Cartilago pilae postopticae, in Stadium X—XI auf der Höhe der Pila prooptica, in Stadium XII auf der Grenze zwischen Pars subcerebralis und Pars praecerebralis der Ethmoidalregion. Dies führt wiederum dazu, dass der in den jüngeren Stadien gewölbte Boden des Cavum cranii in dem fertig ausgebildeten Chondrokranium eben wird.

In Zusammenhang mit den letzten Phasen dieses Vorganges (Stadium VII—IX) laufen Formveränderungen an der Nasenkapsel ab. Der subcerebrale Teil der Kapsel wird hierbei nach vorn verschoben, sodass die Cupula posterior nasi statt kaudal von der vorderen Kante der Pila prooptica rostral von dieser zu liegen kommt, und somit das kurze Septum interorbitale in Erscheinung tritt. Dieses entsteht folglich sekundär oder wird während der Entwicklung vergrössert, was beim Vergleich mit anderen Tieren zu berücksichtigen ist. Durch diese Vorwärtsverschiebung gelangt das Gebiet der Prominentia anterior seitlich an den hintersten Teil des Tectum der Pars praecerebralis. Hierbei ebnet sich die stark gebogene Form des betreffenden Tectumteiles aus, und das Foramen epiphaniale kommt statt an einer seitwärts gerichteten Fläche an den Übergang zwischen dem dorsalwärts und dem lateralwärts gekehrten Teil der Nasenkapsel zu liegen.

Eine andere wichtige Veränderung trifft die Ohrenkapsel. Schon in Stadium V, wo das Blastem der Kapsel noch nicht vollständig ausgebildet ist, ist sie stark zur Seite geneigt, welche Lage bis zu dem Stadium XI beibehalten wird. Zwischen diesem und dem Stadium XII richtet sie sich aber zu der steilen Lage auf, die auch für das erwachsene Tier charakteristisch ist. Sonstige Drehungen der Ohrenkapsel finden während der Entwicklung nicht statt.

Der oft herangezogene Quotient zwischen dem Volumen der Ohrenkapsel und dem der Schädelhöhle ist nach Messungen an zwei Stadien berechnet worden. Für das Stadium XI ist der Wert 1/38, für das Stadium XII 1/25 erhalten worden. Diese grosse Veränderung im Laufe eines verhältnismässig kurzen Entwicklungsabschnittes zeigt die Unzulänglichkeit eines Vergleiches derartiger Quotienten.

Die Basalplatte wird sehr lang, die Ohrenkapsel sehr kurz angelegt. So hat die erstgenannte bereits in dem Stadium V fast dieselbe Länge erreicht wie in

Stadium VIII und sogar Stadium X. Die Beziehung zwischen der vorderen Kante der Ohrenkapsel und dem Planum basale ist dieselbe bei der Anlegung ihrer Blasteme wie in dem voll ausgebildeten Chondrokranium. Die folgende Grössenzunahme der Kapsel findet folglich in dorsaler und kaudaler Richtung statt. Gleichzeitig hiermit verbreitert sich die Pila occipitalis, besonders die Lamina alaris, die rostralwärts strebend sich mit der Ohrenkapsel verbindet. Dieser Vorgang wird ventral durch eine anfangs selbständige Verknorpelung vermittelt in einem sogar selbständig erscheinenden Blastem. Dadurch, dass die Lamina alaris sich ventral weit rostralwärts ausdehnt, wird das Foramen jugulare nach vorn gerichtet.

Die Pila occipitalis entsteht durch die Verschmelzung der Neuralbogen der vier der Occipitalregion zugehörigen Wirbelanlagen. Hierbei entstehen zunächst zwei blastematische Schenkel, die wie bei Ovis und Talpa (Levi 1909) lang — auch nach der Verknorpelung — durch eine Strukturgrenze als selbständige Elemente erkannt werden können.

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Die eingehendsten Untersuchungen über die Beziehung der Chorda dorsalis zur Basalplatte sind von I. P. Tourneux (1911) und F. und I. P. Tourneux (1912) zusammengestellt. Den von diesen Autoren aufgestellten vier Typen wird ein fünfter von Matthes (1923) angeschlossen, der sie in eine morphologische Reihe (1.—5.) ordnet. Ob aber diese Ordnung der phylogenetischen Entwicklung entspricht, bleibt dahingestellt (Stadtmüller 1936). Die Beziehung zwischen der Chorda dorsalis und der Basalplatte entspricht bei den jüngeren Stadien (V—VII) von Procavia dem Typus 3 („intermédiaire entre les types basilaire et retrobasilaire" von Tourneux), der bei Equus, Ovis, Capra, Cavia und Talpa vorkommt. Diese Verhältnisse gehen aber dann bei Procavia im Laufe der Entwicklung in den Typus 2 („basilaire" von Tourneux) über, der bei Bos und Sus vertreten ist. Hieraus scheint hervorzugehen, dass der Typus 3 ein phylogenetisch früheres Stadium als der Typus 2 ist. Der Typus 3 ist bei Procavia dadurch bedingt, dass die Chorda in dem ungegliederten Teil der Basalplatte eingebettet ist und Wirbelkörperanlagen des auximetameren Teiles fehlen.

Das Verhalten der drei Wurzeln des Nervus hypoglossus beim Austreten aus dem Schädel wechselt sehr von Stadium zu Stadium. Oft verhalten sie sich auch verschieden an den beiden Seiten. Im Stadium IV sind die drei Wurzeln fast über die ganze Länge des breiten hinteren Abschnittes des Planum basale verteilt, von Blastem voneinander getrennt, während sie in älteren Stadien nahe am vorderen Rand der Pila occipitalis durch ein mehr oder weniger einheitliches Foramen hypoglossi austreten. Hieraus folgt, dass sie zunächst metamer angelegt werden, und danach zumindesten die zwei hinteren Wurzeln nach vorn verschoben werden. Bei diesem Vorgang, der augenscheinlich schon in Stadium IV eingesetzt hat, eilen die distalen Teile der Wurzeln voraus, da diese fast immer die äussere Mündung des Canalis hypoglossus gemeinsam

verlassen. Nur in einem Falle ist eine Verknorpelung der die Wurzeln trennenden, zurückgebliebenen Gewebspartienen beobachtet worden. Die Variation in dem Verhalten der Hypoglossuswurzeln ist darauf zurückzuführen, dass ihre Verschiebung in den einzelnen Exemplaren und an den beiden Seiten mit verschiedener Geschwindigkeit vor sich geht. Ähnliche Verhältnisse sind bei Halicore (MATTHES 1921), Mus, Ovis (LEVI 1909) festgestellt worden.

Das Studium der blastematischen Anlegung des Primordialkraniums hat in einigen Hinsichten interessante Aufschlüsse gegeben. So wurde die Teilnahme der Hypochordalspangen und Neuralbogen von vier Wirbelanlagen an dem Aufbau der Occipitalregion festgestellt. Dieselbe Zahl fand FRORIEP (1886) für Bos. (Über spätere Literatur s. STADTMÜLLER 1936.)

An einigen Stellen grenzen sich bei Procavia gewisse Blasteme scharf voneinander ab, schon ehe die Verknorpelung einsetzt, und es liegt an der Hand, diesen Differenzierungen eine viel grössere phylogenetische Bedeutung beizumessen als nur dem Auftreten selbständiger Verknorpelungszentren. In dieser Weise grenzt sich das Blastem der Cartilago pilae postopticae von der Lamina trabecularis und der Pila postoptica ab, das Epihyale von dem Stylohyale, das Tectum nasi von dem Paries nasi längs der Verbindungslinie zwischen der Incisura praecribrosa und dem Foramen epiphaniale. In diesem Zusammenhang ist auch die starke Verdünnung des Blastems in dem Gebiet zu nennen, das der Fenestra superior einiger anderer Ungulaten entspricht.

Einige der über die Art der Verknorpelung des Schädels bei Procavia gewonnenen Ergebnisse sollen kurz besprochen werden. Die Parachordalplatte entsteht hier in ihrem vorderen Teil unpaarig bei der einsetzenden Verknorpelung. Wenn diese sich nach hinten ausbreitet, wird die Platte jedoch hier paarig, wie die schon vorhandenen Blasteme. Für andere Säuger ist sowohl paarige wie unpaarige Anlegung nachgewiesen worden (vgl. STADTMÜLLER 1936).

Eine selbständig verknorpelnde Hypophysenplatte ist bei Echidna (GAUP 1908), Tatusia (FAWCETT 1921), Talpa (NORDENBOS 1905, FAWCETT 1916), Lepus (DE BEER 1930), Felis (TERRY 1917), Bos (FAWCETT 1918a), Homo (FAWCETT 1918b) und Suncus (ROUX 1947) bekannt. Dieser Reihe können wir jetzt Procavia anschliessen, bei der sich der betreffende Knorpel zuerst unpaarig kaudal von dem Canalis hypophyseos entwickelt.

Die Entstehung der Nasenkapsel bei Felis (TERRY 1917), Talpa (NORDENBOS 1905) und Lepus (DE BEER 1930) erfolgt in grosser Übereinstimmung. TERRY schloss aus seinen Untersuchungen an Felis, dass da, wo die Cartilago paranasalis sich über den Rand des Paratectalknorpels schiebt, eine gebogene, in das Kapselinnere hineinragende Kante, die Anlage der Crista semicircularis, gebildet wird. Wir können nun die interessante Feststellung machen, dass bei Procavia, wo die genannte Crista fehlt, die Verknor-

pelung des Paries in anderer Weise vor sich geht, indem nicht zwei verschiedene Knorpelstücke längs des Sulcus lateralis anterior, die der Insertionslinie der Crista semicircularis entspricht, zusammenstossen, sondern die Paranasalknorpel sich hier über diese rostralwärts ausbreiten. In derselben Weise entsteht nach TERRY das Ethmoturbinale I da, wo die Cartilago paranasalis sich über den Rand des Antorbitalknorpels schiebt.

Im allgemeinen beginnt die Verknorpelung der Ohrenkapsel an der Aussenseite des Labyrints (Echidna, GAUP 1908; Sorex, DE BEER 1929; Felis, TERRY 1917; Walen, DE BURLET 1913—16; Talpa, NORDENBOS 1904, 1905; Sus, LEBEDKIN 1918) und die Schneckenkapsel wird von hier aus verknorpelt. (Eine Ausnahme ist Talpa, bei der die Schneckenkapsel selbständig verknorpelt.) Bei Procavia setzt die Verknorpelung dagegen an der medialen Fläche in der Pars cochlearis zuerst ein. Dann treten Verknorpelungszentren an der medialen wie an der lateralen Fläche der Pars canalicularis auf, wobei ich nicht entscheiden kann, welche zuerst entsteht. Über die Verknorpelung der Lamina supracapsularis mit der Cartilago supraoccipitalis und dem Tectum posterius geben die von mir untersuchten Stadien wenig Aufschluss. Es kann nur gesagt werden, dass dieser Vorgang hier unabhängig von der Verknorpelung in der Pila occipitalis vor sich geht. Bei Felis (TERRY 1917), Talpa (NORDENBOS 1905) und Lepus (DE BEER 1930) verknorpelt die Lamina supracapsularis von zwei Zentren aus, der Lamina parietalis und der Cartilago supraoccipitalis. Sie unterscheiden sich nur hinsichtlich des Zeitpunktes, zu dem die zunächst selbständigen Knorpelplatten sich miteinander und mit anderen Knorpelteilen verbinden. Bei Echidna (GAUP 1908) verknorpelt die ganze Lamina supracapsularis in einem Stück. Ihr unvermitteltes Auftreten bei Procavia könnte auf einer ähnlichen Entstehungsweise beruhen.

Die blastematische Hyalspange ist wie gewöhnlich bei Tetrapoda in ihr dorsales Ende gespalten. Für diesen dorsalen Teil, der sich schon vor der Verknorpelung von dem Rest absetzt, wurde die Bezeichnung Stylohyale (vgl. STADTMÜLLER 1936) verwendet, während das ventral folgende Element Epihyale genannt wurde. Der medial gerichtete Schenkel verbindet sich eng mit dem Crus longum incudis (vgl. FUCHS 1905) und hört mit dem Stapesblastem auf. Das Mesenchym des lateralen Schenkels, das Laterohyale, wird in Gegensatz zu dem des medialen viel später verdichtet. Epihyale und Stylohyale verknorpeln je zu einem Stück. Bei dem letztgenannten setzt dieser Vorgang ventral an dem künftigen Ligament ein und breitet sich langsam dorsalwärts aus. Hiernach verschwindet der mediale Schenkel bis auf den Stapes. Zuletzt verknorpelt das Laterohyale und danach erst der angrenzende Teil der Crista parotica, wodurch das Hyale an der Ohrenkapsel befestigt wird.

Das bearbeitete Material hat gute Möglichkeiten gegeben, die Anlage und Entwicklung des Stapes zu studieren. Für die umfangreiche Literatur ver-

weise ich auf die Zusammenfassungen von GAUP (1899) und VAN DER CLAAUW (1924). Bei Procavia liegt in Stadium V das durchbohrte Blastem des Stapes dem Ohrenkapselblastem dicht an, lässt sich aber von diesem unterscheiden. Wenn die Verknorpelung zwischen Stadium VII und VIII einsetzt fängt sie in den beiden Crura an und setzt sich in dem zentralen Teil der künftigen Fussplatte fort. In dem Stadium VIII hat sich der so entstandene Knorpelkern scharf von der medial und perifer davon gelagerten Blastemmasse abgesetzt, die früher ohne jegliche Grenze in das Ohrenkapselblastem überging, hier aber angefangen hat, sich als zweites Blastem der Fussplatte von dem Ohrenkapselblastem abzugrenzen. Die Verknorpelung geht also hier von einem einheitlichen (oder paarigen!) Zentrum aus. Erst zwischen Stadium X und XI fängt der obengenannte perifere und mediale Teil der Fussplatte an zu verknorpeln. Dieser Vorgang setzt an der scharf markierten Grenze zwischen dem verknorpelten und dem unverknorpelten Teil der Fussplatte ein und breitet sich von hier allmählich aus. Durch Zuwachs des hyoiden Anteils des Stapes nach seiner Verknorpelung treibt dieser den von dem Ohrenkapselblastem stammenden Anteil medialwärts vor sich her und macht in dem Stadium XII einen viel grösseren Teil der Gesamtmasse des Stapes aus als in früheren Stadien. Auch in dem Stadium XIV und in einem Embryo von 60 mm Scheitel-Steiss-Länge können diese zwei Knorpelkomponenten unterschieden werden. In dem letztgenannten Embryo hat sich der mediale Anteil des Stapes in der Ebene der Fussplatte stark verbreitert, sodass er einen wesentlichen Teil von letzterer ausmacht. Mit dem Schlussergebnis dieser Entwicklung, wie es in dem zuletzt besprochenen Embryo vorliegt, stimmt der Stapes bei Globiocephalus (SCHREIBER 1916) so weitgehend überein, dass ohne weiteres derselbe Entwicklungsmodus hier vorausgesetzt werden kann.

Aus zweierlei Gründen lässt sich die doppelte Anlegung des Stapes hier verfolgen: 1. weil die zwei Anlagen sich während der ganzen Entwicklung gut gegen einander abgrenzen, 2. weil die beiden Anlagen zu ganz verschiedenen Zeiten verknorpeln.

Über die Herkunft der Stapesanlage von dem Hyoidbogen scheint in späterer Zeit allgemeine Einigkeit zu herrschen. Auch die Entstehung der Fussplatte von der Stapesanlage aus scheint allgemein angenommen zu werden. Das Ohrenkapselblastem nimmt dabei nicht teil, sondern sein sich medial des Stapes befindender Teil wird in Bindegewebe umgewandelt. Dieser Vorgang kann sich aber verschieden gestalten. 1. Das betreffende Blastemgebiet geht direkt in Bindegewebe über z. B. bei Mus (JENKINSON 1911). 2. Das Blastem wird zu Vorknorpel bei Lepus (DREYFUSS 1893), zu einem „nahezu jungknorpeligen Gewebe" bei Ovis (DREYFUSS) oder zu „Jungknorpel" bei Lepus (FUCHS 1905), das in sämtlichen Fällen dann in Bindegewebe umgewandelt wird. 3. Das Blastem wird bei Homo „richtiges junges Knorpelgewebe" (DREYFUSS), das dann wiederum einer Umwandlung in Bindegewebe

unterliegt. Diese Reihe zeigt eine zunehmende Tendenz zur Knorpelbildung in dem betreffenden Gebiet. Das Knorpelgewebe wird, wenn es zur Ausbildung kommt, dann wieder abgebaut. Dies deutet an, dass bei den Vorfahren der rezenten Säugetiere der Stapes aus zwei Anlagen, einer hyoiden und einer dem Ohrenkapselblastem entstammenden aufgebaut wurde, ein Zustand der bei Globiocephalus[1] und Procavia immer noch besteht. Die Verhältnisse, die GAUP (1908) bei Echidna beschreibt, dass die Fussplatte sich durch Apposition neuen Knorpels vergrössert, der deutlich gegen den alten abzugrenzen ist und dem umgebenden Bindegewebe entstammt, sind von dem reduzierten phylogenetischen Zustand, der z. B. von Mus repräsentiert wird, abzuleiten.

Wird das Chondrokranium von Procavia mit denen anderer Placentalier verglichen, fällt die schwache Ausbildung seines hinteren Abschnittes auf, infolge des Fehlens mehrerer Commissuren. So vermissen wir eine Commissura basicochlearis anterior, eine Commissura alicochlearis und eine Commissura orbitoparietalis. Die aufrecht stehenden Ohrenkapseln sind dafür sehr stark medial zusammengedrängt. Weiter ist die Verbindung zwischen der Occipitalregion und der Ohrenkapsel sehr innig. Der Pars praecerebralis der Nasenkapsel fehlen Fenestrationen.

Schliesslich möchte ich kurz auf einige Verhältnisse aufmerksam machen, die von besonderem Interesse sind.

An der Ala temporalis findet sich bei Procavia ein Foramen rotundum, das sonst bei Perameles, Didelphys, Carnivora und Primates vorkommt und bisher bei keinem Ungulat beobachtet worden ist. Auffallend ist weiter die Übereinstimmung der Ala temporalis bei Procavia mit der von Felis domestica (TERRY 1917). Schwer zu verstehen ist der offensichtliche Mangel an Ähnlichkeit zwischen der Ala temporalis von Felis domestica (TERRY 1917) und der von Felis catus (FAWCETT 1918).

Die Cartilago pilae postopticae zeigt eine auffallend selbständige Entwicklung, wie dies hinsichtlich der Verknorpelung für ein entsprechend gelagertes und als Ala hypochiasmatica benanntes Element schon von FAWCETT (1921) bei Tatusia nachgewiesen ist. Dasselbe gilt für die Lamina hypochiasmatica bei Lepus (DE BEER 1930) und das in derselben Weise benannte Element bei Eremitalpa, Suncus und Elephantulus (ROUX 1947). DE BEER sieht in den Laminae hypochiasmaticae und den Processus paroptici identische Bildungen, obwohl die einen den Pilae proopticae, die anderen den Pilae postopticae angeschlossen werden. Da diese Identität wohl noch nicht bewiesen ist, habe ich die neutrale Benennung Cartilago pila postoptica angewandt, um damit nur ihre Lage anzugeben. Processus paroptici

[1] Die von SCHREIBER angegebene Struktur, „die Grundsubstanz auf ein Balkenwerk reduziert", des medialen Stapesanteiles bei Globiocephalus könnte auch als Anzeichen einer schwächeren Ausbildung aufgefasst werden.

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kommen bei vielen Säugern vor (vgl. STADTMÜLLER 1936). Wie bei Procavia dienen sie bei Tatusia (FAWCETT 1921) als Insertionsstelle der Gruppe von Musculus recti. Auch bei Sus (MEAD 1909), Canis (OLMSTEAD 1911) und Elephantulus (ROUX 1947) inserieren einige Augenmuskeln an diesen kleinen Fortsätzen. Dasselbe gibt HONIGMANN (1917) für Megaptera an und nennt dabei besonders Musculus obliquus inferior. Allerdings findet sich der Processus paropticus hier in jüngeren Stadien zwischen den beiden Wurzeln der Ala orbitalis in älteren dagegen lateral von der vorderen Wurzel, also in anderer Lage als bei Procavia und Tatusia. Die Laminae hypochiasmaticae bei Lepus werden von VOIT (1909) für homolog dem Processus hypochiasmaticus bei Lacerta[1] angesehen. Dass es sich hinsichtlich der Cartilago pila postoptica um einen Neuerwerb der Mammalien handeln sollte, ist wenig wahrscheinlich. Ein entsprechend gelagertes und sich entwickelndes Element scheint allerdings den recenten Reptilien und Amphibien zu fehlen. Wird sowohl die auffällig selbständige Entwicklung wie die Insertion der Augenmuskeln berücksichtigt, fällt bei einem Vergleich die Übereinstimmung mit dem Augenstielknorpel der Selachier zunächst auf.

Die morphologische Bedeutung des kleinen spät erscheinenden Knorpelelementes am Hinterrand der Ala orbitalis (Fig. 69, y) ist schwer zu beurteilen, eben weil es so klein ist. Der folgende Deutungsversuch gründet sich darauf, dass es in seiner Längsrichtung verlängert das Foramen opticum in zwei Teile aufteilen würde. Das genannte Foramen dient als Durchtrittsstelle für Nervus opticus und Arteria ophtalmica. Die genannte Aufteilung würde also zu einem hypothetischen Stadium führen können, in dem Nervus opticus und Arteria ophtalmica durch verschiedene Foramina die Schädelhöhle verlassen würden. Dieser Zustand liegt bei gewissen Schildkröten (Emys, KUNKEL 1912; Chrysemys, SHANER 1926) vor, bei denen die Pila metoptica basal durch ein Foramen für die Arteria ophtalmica durchbohrt ist. Der kleine Knorpelstab könnte somit dem vorderen Schenkel der Pila metoptica der genannten Chelonia entsprechen. Eine Reduktion eben des vorderen Schenkels dürfte im Zusammenhang mit der stattgefundenen seitlichen Verlagerung der Augen bei den Mammalia stehen.

Eine verhältnismässig sehr kurze Spina mesethmoidalis ist bei Procavia vorhanden. Diese Bildung kommt bei Manatus, Halicore (MATTHES 1912, 1921) und Walen (DE BURLET 1914a, b, HONIGMANN 1917) vor. Dass eine ähnliche Bildung auch in dem embryonalen Elefanten vorliegt, scheint aus einer Abbildung EALES' (1926—28) hervorzugehen.

Das Fehlen einer Crista semicircularis bei Procavia haben wir schon im Zusammenhang mit der Art der Verknorpelung der Nasenkapsel besprochen. Interessant ist, dass dieses Gebilde auch bei Equus vermisst

[1] DE BEER (1937) drückt denselben Gedanken allerdings mit grösserer Reservation aus. Über Einwände gegen diese Homologisierung vgl. MICHELSSON 1922.

wird (SÖRENSEN 1931). Es liegt an der Hand, die Ursache hierzu in einem ähnlichen Entwicklungsmodus des Paries nasi bei Equus wie bei Procavia zu sehen.

Eine weitere Übereinstimmung zeigt Procavia mit dem Pferd, das auch eine sehr steil stehende Ohrenkapsel und vorn schmale Basalplatte besitzt (MUGGIA 1931, SÖRENSEN 1931)[1]. Bei beiden bildet die Ohrenkapsel Seitenwand der Schädelhöhle und nicht Boden. Nach VOIT (1909) macht die Ohrenkapsel im Laufe der phylogenetischen Entwicklung der Mammalia Drehungen um drei verschiedene Achsen durch. Eine von diesen soll zu der seitlichen Neigung der Kapsel führen. Wie die Entwicklung lehrt, ist bei Procavia die aufrechte Lagerung der Ohrenkapsel keineswegs ein primärer Charakter und dürfte auch nicht phylogenetisch als primär aufzufassen sein. Auch hier hat man Anlass zu vermuten, dass die Entwicklung beim Pferd mit der von Procavia übereinstimmt.

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In dem verknöcherten Schädel von Procavia läuft der Nervus facialis rostrolateral von dem dorsalen Teil des Hyoids, anstatt wie gewöhnlich bei Säugetieren laterokaudal (HOWES 1896, VAN KAMPEN 1905). DE BEER (1937) versucht dies damit zu erklären, dass das Laterohyale in anderer Richtung als z. B. bei Lepus gewachsen ist, und dass der Nervus facialis über das noch freie Ende des Knorpels hat hinübergleiten können. Dies ist aber nicht der Fall, da in sämtlichen hier beschriebenen Stadien die gewöhnlichen Beziehungen zwischen Hyale und Nervus facialis bestehen, wie auch in einem Stadium von 80 mm. Länge festgestellt wurde. Diese Verhältnisse sind auf die eigenartige Form des kaudal gerichteten Stylohyale zurückzuführen (vgl. S. 361 und Fig. 47). Seine proximalen Teile, Querspange und Verbindungsspange, werden wahrscheinlich bei der Verknöcherung in das Os temporale aufgenommen. Hierdurch scheint der Nervus facialis *rostral* von dem Processus styloideus auszutreten.

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[1] Letzterer Charakter ist auch bei Sus (MEAD 1909) vorhanden.

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VERZEICHNIS DER ABKÜRZUNGEN.

A. carot. int. Arteria carotis interna.
Ala orb. Ala orbitalis.
Ala temp. Ala temporalis.
A. max. int. Arteria maxillaris interna.
Amp. lat. Ampulla lateralis.
Amp. pos. Ampulla posterior.
Anl. d. Spina mes. ethm. Anlage der Spina mesethmoidalis.
A. opht. Arteria ophtalmica.
A. staped. Arteria stapedialis.
Atrioturb. Atrioturbinale.
Ausf.-gang d. Gland. nas. lat. Ausführungsgang der Glandula nasalis lateralis.
Blast. d. Tympanic. Blastem des Tympanicum.
Blast. d. Cart. duct. nasopalat. Blastem der Cartilago ductus nasopalatini.
Blast. d. Stapes. Blastem des Stapes.
Can. hypogl. Canalis hypoglossi.
Can. hypophys. Canalis hypophyseos.
Can. membr. ant. Canalis membranaseus anterior.
Can. membr. lat. Canalis membranaseus lateralis.
Can. membr. post. Canalis membranaseus posterior.
Can. semic. ant. Canalis semicircularis anterior.
Can. semic. lat. Canalis semicircularis lateralis.
Can. semic. post. Canalis semicircularis posterior.
Can. utric.-sacc. Canalis utriculo-saccularis.
Caput mall. Caput mallei.
Cart, auric. Cartilago auricularis.
Cart. cupul. Cartilago cupularis.
Cart. duct. nasopalat. Cartilago ductus nasopalatini.
Cart. Meckel. Meckelscher Knorpel.
Cart. papill. palat. Cartilago papillae palatinae.
Cart. parasept. Cartilago paraseptalis.
Cart. pil. postopt. Cartilago pilae postopticae.
Cart. pteryg. Cartilago pterygoideus.
Cart. Reich. Reichertscher Knorpel.
Cart. supraoccip. Cartilago supraoccipitalis.
Cav supracochl. Cavum supracochlearis.
Cav. tymp. Cavum tympani.
Chorda dors. Chorda dorsalis.
Chorda tymp. Chorda tympani.
Comm. basicochl. Commissura basicochlearis.
Comm. caps.-par. Commissura capsulo-parietalis.
Comm. occip.-caps. Commissura occipitocapsularis.
Comm. sphen.-ethm. Commissura sphenoethmoidalis.
Comm. suprafac. Commissura suprafacialis.
Concha front. Concha frontalis.
Cond. occip. Condylus occipitalis.
Corpus incud. Corpus incudis.
Crista amp. lat. Crista ampularis lateralis.
Crista amp. post. Crista ampularis posterior.
Crista horiz. Crista horizontalis.
Crista intercribr. Crista intercribrosa.
Crista parot. Crista parotica.
Crista praecribr. Crista praecribrosa.
Crista proot. Crista prootica.
Crista trab. Crista trabecularis.
Cupul. post. Cupula posterior.
Crus ant. Crus anterius.
Crus comm. Crus commune.
Crus long. Crus longum.
Crus post. Crus posterius.
Dens epistr. Dens epistropheus.
Duct. cochl. Ductus cochlearis.
Duct. endolymph. Ductus endolymphaticus.
Duct. nasolac. Ductus nasolacrimalis.
Duct. nasophar. Ductus nasopharyngeus.
Duct. reun. Ductus reuniens.
Epistroph. Epistropheus.
Ethmoturb. I—III. Ethmoturbinale I—III.
Fen. bas. Fenestra basalis.
Fen. vestib. Fenestra vestibuli.
Fil. olfact. Fila olfactoria.
Fiss. alisphen. Fissura alisphenoidea.
Fiss, basicochl. Fissura basicochlearis.
Fiss. caps.-par. Fissura capsuloparietalis.
Fiss. occip.-caps. Fissura occipitocapsularis.
Fiss, orb.-nas. Fissura orbitonasalis.
For. acust. Foramen acusticum.
For. acust. sup. Foramen acusticum superius.
For. acust. inf. Foramen acusticum inferius.
For. alisphen. Foramen alisphenoideum.
For. endolymph. Foramen endolymphaticum.

For. epiphan. Foramen epiphaniale.
For. fac. Foramen faciale.
For. fac. prim. Foramen faciale primarius.
For. fac. sec. Foramen faciale secundarius.
For. hypogl. Foramen hypoglossi.
For. jugal. Foramen jugale.
For. opt. Foramen opticum.
For. perilymph. Foramen perilymphaticum.
For. rotund. Foramen rotundum.
Forts. d. Mall.-Ink. Fortsatz des Malleus-Inkus.

Foss. hypophys. Fossa hypophysea.
Foss. incud. Fossa incudis.
Foss. muscl. stap. Fossa musculi stapedii.
Foss, subarc. ant. Fossa subarcuata anterior.
Foss. subarc. lat. Fossa subarcuata lateral
Fov. gen. Fovea genicularis.
Fov. muscl. maj. Fovea muscularis major.
Fusspl. d. Stapes. Fussplatte des Stapes.
Ggl. access. Chord. tymp. Ganglion accessorium der Chorda tympani.

Ggl. genic. Ganglion geniculi.
Ggl. jugul. Ganglion jugulare.
Ggl. petr. Ganglion petrosum.
Ggl. semilun. Ganglion semilunare.
Ggl. spir. Ganglion spirale.
Ggl. super. Ganglion superius
Ggl. vestib. Ganglion vestibuli.
Gland. nas. lat. Glandula nasalis lateralis.
Hyale m. Lig. Hyale mit Ligament.
Hypophys.-Platte. Hypophysenplatte.
Incis. intercond. Incisura intercondyloidea.
Incis. sup. Incisura superior.
Komplex d. Mall.-Inc. Komplex des Malleus-Incus.

Lam. alar. Lamina alaris.
Lam. asc. alae temp. Lamina ascendens alae temporalis.
Lam. cribr. Lamina cribrosa.
Lam. infr.-cribr. Lamina infracribrosa.
Lam. pariet. Lamina parietalis.
Lam. pteryg. Lamina pterygoidea.
Lam. supracaps. Lamina supracapsularis.
Lam. supraoccip. Lamina supraoccipitalis.
Lam. trab. Lamina trabecularis.
Lam. transv. ant. Lamina transversalis anterior.
Lam. transv. post. Lamina transversalis posterior.
Lat.-hyale Laterohyale.
Lob. olfact. Lobus olfactorius.
Macula utric. Macula utriculi.
Manubr. Mall. Manubrium Mallei.
Massa angul. Massa angularis.
Maxilloturb. Maxilloturbinale.
Meat, audit. ext. Meatus auditivus externus.
Membr. tymp. Membrana tympani.
Musc. staped. Musculus stapedius.
Musc. tensor tymp. Musculus tensor tympani.

Nasoturb. Nasoturbinale.
N. abd. Nervus abducens.
N. fac. Nervus facialis.
N. glossoph. Nervus glossopharyngeus.
N. hypogl. Nervus hypoglossus.
N. oculum. Nervus ocolumotorius.
N. petr. sup. maj. Nervus petrosus superfacialis major.

N. trig. I—III Nervus trigeminus I—III
N. trochl. Nervus trochlearis.
Nervus vagus Nervus vagus.
N. vid. Nervus videanus.
Occip.-wirb. Occipitalwirbel.
Org. Jacobs. Jacobsonsches Organ.
Ohrenkaps. Ohrenkapsel.
Ohrenkaps.-blast. Ohrenkapselblastem.
Pila occip. Pila occipitalis.
Pila postopt. Pila postoptica.
Pila proopt. Pila prooptica.
Plan. bas. Planum basale.
Proc. alar. Processus alaris.
Proc. alar. inf. Processus alaris inferior.
Proc. alar. sup. Processus alaris superior.
Proc. lat. Processus lateralis.
Proc. med. lat. Processus medialis lateralis.
Proc. med. ventr. Processus medialis ventralis.

Proc. palat. med. d. Incisions Processus palatinalis medialis des Incisivus.
Proc. parachon. Processus parachondyloideus.
Proc. paropt. Processus paropticus.
Proc. pteryg. Processus pterygoideus.
Proc. pteryg. lat. Processus pterygoideus lateralis.
Proc. pteryg. med. Processus pterygoideus medialis.
Prom. ant. Prominentia anterior.
Prom. cochl. inf. Prominentia cochlearis inferior.

Prom. crur. comm. Prominentia cruris communis.
Prom. paracrib. Prominentia paracribrosa.
Prom. post. Prominentia posterior.
Prom. semic. ant. Prominentia semicircularis anterior.
Prom. semic. post. Prominentia semicircularis posterior.
Prom. sup. Prominentia superior.
Prom. supraconch. Prominentia supraconchalis.
Prom. utric.-amp. ant. Prominentia utriculoampularis anterior.
Prom. utric.-amp. post. Prominentia utriculoampullaris posterior.
Rad. N. fac. Wurzel des Nervus facialis.
Rad. N. hypogl. Wurzel des Nervus hypoglossus.
Rad. N. trig. Wurzel des Nervus trigeminus.
Ram. orb. Ramus orbitalis.
Recess. jug. Recessus jugularis.
Recess. post. Recessus posterior.
Recess. utric. Recessus utricularis.
Rinne d. N. fac. Rinne des Nervus facialis.
Sacc, endolymph. Sacculus endolymphaticus.
Sacc, perilymph. Sacculus perilymphaticus.
Sehne d. Musc. staped. Sehne des Musculus stapedialis.
Sept. interorb. Septum interorbitale.
Sept. metacochl. Septum metacochleare.
Sept. nasi. Septum nasi.
Sept. spir. Septum spirale.
Sin. post. Sinus posterior.
Sin. sigm. Sinus sigmoideus.
Spangen d. Lam. cribr. Spangen der Lamina cribrosa.
Spina alar. Spina alaris.
Spina mesethm. Spina mesethmoidalis.
Sulc. carot. Sulcus caroticus.
Sulc. horiz. Sulcus horizontalis.
Sulc. infrasept. Sulcus infraseptalis.
Sulc. lat. ant. Sulcus lateralis anterior.
Sulc. lat. post. Sulcus lateralis posterior.
Sulc. N. fac. Sulcus Nervi facialis.
Sulc. sept. Sulcus septalis.
Sulc. suprasept. Sulcus supraseptalis.
Tectum post. Tectum posterius.
Tegmen tymp. Tegmen tympani.
Tuba audit. Tuba auditiva.
Ven. jugul. int. Vena jugularis interna.
Ven. cap. lat. Vena capitis lateralis.
Ventr. Münd. d. can. hypophys. Ventrale Mündung des Canalis hypophyseus.

A RAPID METHOD FOR SELECTIVE SILVER STAINING OF NERVE FIBRES AND NERVE ENDINGS IN MOUNTED PARAFFIN SECTIONS

BY

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Abstracts. The staining described in this paper fundamentally is performed by two manipulations, namely (1) the treatment of deparaffinized sections for about fifteen minutes in a solution containing 15 per cent silver nitrate, 10 per cent potassium nitrate and 0.05 per cent glycine, and (2) the reduction for one minute in a solution of 1 per cent pyrogallol, 55 per cent ethyl alcohol and a trace (0.002 per cent) of nitric acid. After toning, dehydrating and mounting in the usual manner the sections generally are ready for examinations within less than an hour. The method is available for specimens fixed in the ordinary fixatives but those containing oxidizing metal compounds. The procedure is discussed from a theoretical point of view and some results are shown in photomicrographs.

Since RAMÓN Y CAJAL (1903) and BIELSCHOWSKY (1902) in the beginning of the century introduced their well-known silver nitrate methods for demonstrating neurofibrils, innumerable more or less complicated variants have been elaborated in order to improve the staining results and to adapt the methods to various purposes and different specimens. Nevertheless, although the results sometimes are very good indeed, undoubtedly the "protargol" method published by BODIAN (1936) is superior to all silver nitrate methods hitherto proposed. Since the autumn of 1947, however, "protargol" may not be manufactured anywhere. At least I have not been able to get any sample of this preparation. Consequently I was forced to return to the silver nitrate methods and working with these methods I found it possible to obtain excellent results in a rather simple way.

A. THE SILVER STAINING FROM A THEORETICAL POINT OF VIEW.

Most methods used in the microscopical staining technique are empirical and must be so because very little seems to be known as to the physical and chemical alterations, which take place during the fixation and the treatments of fixed tissues with solutions of mordants or stains.

This is unfortunate, as a proper understanding of what happens would save time by the elaboration of new and better methods and—concerning the silver staining—by adaptation of the methods to different specimens and by finding out the causes of accidental failures.

Regarding the procedure of silver staining it is possible, however, to discuss the influence of at least some fundamental factors.

This procedure consists of what I would call (1) the process of mordanting, (2) the process of reduction and (3) the process of toning and intensifying.

1. THE MORDANTING.

According to LIESEGANG (1911) minute "germs" ("*Keim*") or—in colloidal chemical terms—"nuclei" of reduced, metallic silver are formed, when tissues are treated with silver nitrate, and these "nuclei" are enlarged by the reduction of the argentic ions during the treatment with a photographical developer, thus forming the visible stain.

In fact no silver staining occurs unless sections or blocks have assumed the very light yellow-brown tint, which is the visible effect of the formation of reduced silver particles or silver "nuclei", and which is most easily observable where there are great amounts of nerve fibres.

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As UNNA (1916) pointed out the proteins are precipitated by silver nitrate forming white "silver albuminate" which soon becomes brown and finally black by the reduction power of light, or—even in the dark—by the action of ubiquitous reducing substances in the tissues.

After fixation the reduction property of the tissues remains, but the reduction power is considerably altered. The alteration is greatly depending upon the fixative used.

Suppossing the proteins are coagulated by heat or by a chemically indifferent fixative, as for instance ethyl alcohol, the reduction power is much weaker than is the reduction power of proteins fixed in formol. If, however, tissues fixed in alcohol afterwards are treated with formol the reduction potential is considerably increased. Hence the formaldehyde does not act as a fixative only, but also as a mordant.

Many other compounds act in a similar way and have also been used as intensifiers of the reduction power, so for instance chloral hydrate, pyridine and ammoniated alcohol. To my experience, however, a *general* increasing of the reduction potential means an advantage in a few and particular cases only.

The indispensable *selectivity* of the staining of nerve fibres presumes that there is a *difference* in the reduction potentials. The nerve fibres necessarily must contain a more powerfully reducing substance, generally referred to as "argyrophilic", than do the non-nervous tissue elements. If there is no such difference apparantly neither an increasing nor a decreasing of the *general* reduction power could improve the staining result.

To some degree, however, the actual distribution of the silver "nuclei" is depending not only upon the natural distribution of more or less powerfully reducing substances, but also upon the hydrogen ion concentration.

Regarding the importance of the hydrogen ion concentration I agree with SILVER (1942) and HOLMES (1943).

In many respects the very interesting hypothesis formulated by SILVER about

factors controlling the silver staining is verified, I believe, by the practical results I have obtained myself. However, some of the most important of these factors: the reduction-oxidation potentials of the tissue substances and the formation of "nuclei" of reduced silver by the action of these substances even in the dark, as well as the dependence of the reduction-oxidation potentials upon the hydrogen ion concentration, SILVER might have perfectly overlooked.

Basic compounds counteract the *differentiated* formation of "nuclei" and the *selective* staining of nerve fibres. Acids (nitric acid in formol) on the contrary, to a certain degree suppress the formation of "nuclei" in and the staining of the non-nervous tissue elements leaving the stainability of the nerve fibres untouched.

The argyrophilic substances of the nerve fibres are more or less blocked by for instance potassium dichromate. They easily react not only with argentic ions but also with other cations of heavy metals. Hence specimens fixed in chromic acid, dichromates, mercuric chloride or osmic acid are not available for silver staining of nerve fibres.

In most methods the time of the mordanting with silver nitrate has been stated to several days at 37° C. However, as stated by WILLIS (1945) a quite sufficient amount of silver "nuclei" is generally formed within a few minutes. By a prolongation of the time of the mordanting the amount of silver "nuclei" is increased not only in the nerve fibres but also in every other tissue structure. Speaking in photographic terms such a prolongation of time, however, means a disadvantageous "over-exposure".

The result of the exposure of a photographic plate is depending upon the two main variables: time and light. In a similar way the result of the mordanting of a section is depending upon time and temperature. At 20° C a suitable time of mordanting is about 15 minutes. At 40° C quite the same result is obtained within 2—3 minutes. Hence the temperature always must be controlled and the mordanting time adapted to the temperature used.

I always obtained the very best results by mordanting in a neutral silver nitrate solution. Chemically pure silver nitrate, guaranteed free from acids (neutral to litmus) may contain, however, just traces of acids not perceivable by use of litmus. By the addition of small amounts of glycine, which acts as a buffer, such deleterious traces of acids are eliminated.

2. THE REDUCTION.

As stated above one of the fundamental factors in the process of silver staining of nerve fibres is the silver "nuclei" formed during the mordanting. Another fundamental presumption is the presence of argentic ions, which really constitute what could be called "the potential stain". Without the co-existence of "nuclei" and argentic ions no silver nitrate staining of nerve fibres is possible.

The mechanism of the silver staining can be demonstrated in a very simple way. When any figure or line is drawn on a slide, using a piece of silver (for instance a silver coin) as pen, the slide immersed in a silver nitrate solution and without rinsing transferred to a pyrogallol solution, the drawing is distinctly stained. The same result is obtained by using any other metal pencil, which by the drawing leaves invisible metal fragments on the slide. Hence the silver "nuclei" do not act because they consist of silver, but because they are negatively electrically charged and able to adsorb the positively electrically charged argentic ions. The reason why a *selective* staining of nerve fibres seems to be unobtainable by mordanting with any other reducible metal compound than silver nitrate is the inability of the firts mentioned compound to form "nuclei" *preferably* in the nerve fibres.

Regarding the selective staining of nerve fibres I am not able to support the theory advanced by SEKI (1940) about the importance of the two factors: suitable density and deficiency of protective colloids.

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It must always be remembered (1) that the silver "stain" consists of silver molecules formed by the reduction of argentic ions, (2) that the section therefore must contain a sufficient great amount of argentic ions, (3) that the argentic ions, being positively charged, to some degree are adsorbed to the negatively charged silver "nuclei", (4) that the *adsorbed* argentic ions by the action of the reducing solution are transformed to insoluble silver molecules, which by cohesion are aggregated to the silver "nuclei", (5) that the silver "nuclei" thus are growing to a more or less visible stain during the reduction and (6) that all argentic ions, which are *not adsorbed* prior to *or during* the process of reduction are transformed to silver molecules flocculating to silver precipitates anywhere. To a major part the final "stain" undoubtedly is formed by argentic ions, which are adsorbed to and reduced at the growing "nuclei" *during the reduction process itself.*

Moreover it must be remembered that the *selective* staining of nerve fibres necessarily presumes that there is a greater amount of silver "nuclei" and of adsorbed argentic ions in these fibres than in the non-nervous tissue elements.

Hence failure in staining always is due (1) either to lack of such a greater amount of "nuclei" in the nerve fibres (due to a lack of stainability) *(2) or to a deficiency or absence of argentic ions.*

The importance of a sufficient amount of argentic ions is most strikingly demonstrated in such cases where an especially great amount of silver nitrate has been stored in a bubble in the section and thus caused a particularly intensive staining att this place (Fig. 1). Further, if the argentic ions are too readily washed out, when a section is treated with the pyrogallol solution, no nerve fibres at all are visibly stained *in spite of* a sufficient amount of "nuclei", but when the pyrogallol solution is heated, the nerve fibres in such cases are intensely stained!

Evidently the process of reduction is by no means a simple one, nor unimportant.

Nevertheless only very few variants have been suggested as to the method of reduction. Hydroquinone, sometimes with the addition of sodium bisulphite or sodium sulphite, or pyrogallol with the addition of formol, have been very steadily used as reducers. CAJAL (1926), however, proposed hydroquinone, formol and acetone in one of his methods, and DAVENPORT (1929) a reducer containing pyrogallol, formol and (unfortunately) very strong ethyl alcohol.

Regarding the factors controlling the process of reduction I have found the following.

If a drop of a silver nitrate solution is placed on a slide and just a very small crystal of any of the developers commonly used in the photography is added to the border of the drop, the formation of the silver precipitate can be examined under the microscope.

Hydroquinone or metol added in this way involves the formation of uniformly distributed, granulated precipitates, which are deposited anywhere in the same rate as the reducer by diffusion spreads out in the silver nitrate solution.

Pyrocatechin and pyrogallol at the first contact with the silver nitrate also form granulated precipitates, but as these reducers diffuse into the silver nitrate solution, the silver particles are not irregularly deposited but precipitated as slender, coiling threads, which *grow* by further addition of silver molecules to the points of the threads. Evidently the argentic ions are *successively* adsorbed to and reduced at the end of the threads.

Hence theoretically pyrocatechin and pyrogallol by their capability to form structurated instead of irregularly scattered precipitates would be the most suitable reducers for the purpose. As a matter of fact only pyrogallol (or pyrocatechin although not with the same good result) could be used as reducer in the procedure described below.

The reason or rather one of the reasons why pyrocatechin and pyrogallol but not hydroquinone or metol are able to form structurated precipitates might be, I presumed, that the first mentioned compounds reduce more slowly than do the last mentioned.

As is well known only uniformly distributed small crystals are formed when a saturated solution of a crystallizable compound is *rapidly* evaporated, but when the evaporation is sufficiently delayed a few crystals can be made to *grow* by a slow and systematic addition of the depositing molecules.

As the silver "nuclei" are ubiquitous and only preferably placed in the nerve fibres, the desired *selective* staining of nerve fibres could scarcely be obtained otherwise than by a washing out of the "potential stain" from the structures which should be unstained or poorly stained, and such a washing out presumes that the argentic ions get *time* to leave these structures previous to the trans-

formation to "stain". As a matter of fact a *momentaneous* reduction by hydroquinone, metol or pyrogallol only results in a rather uniform staining of *all* tissue structures. On the other hand by using pyrocatechin, which reduces very slowly, a *selective* but poor staining of nerve fibres is obtainable.

Consequently I directed the investigations on factors influencing the reduction rate.

Using equal amounts and concentrations of solutions at the same temperature I tried to approximately determine the time interval between the addition of silver nitrate to the reducer and the first appearance of the silver precipitate.

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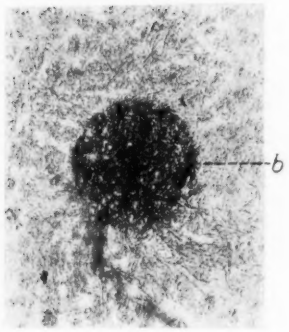

Fig. 1. The effect of a great amount of argentic ions, which have been stored in a bubble, *b*, and caused a particularly intensive staining at this place. Medulla oblongata, rabbit. Photomicrograph.

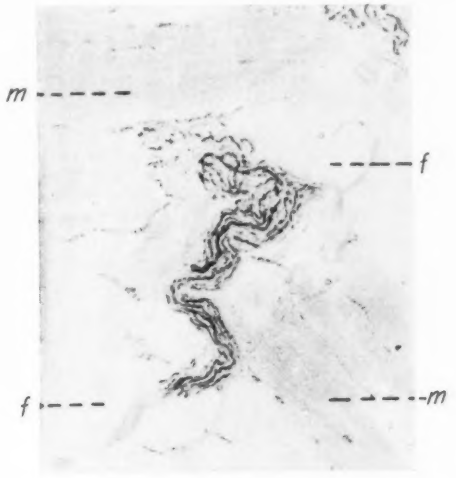

Fig. 2. The highest degree of selectivity obtained by a delayed reduction. Nerve endings in striated muscles from the tongue of a cat. *m*, striated muscle fibres; *f*, fat tissue. Photomicrograph.

The delay of the precipitation by using absolute ethyl alcohol instead of water as solvent for the pyrogallol was found to be in the ratio of about 4: 1. By addition of weak oxidizers as sodium-, potassium- or ammonium nitrate or potassium chlorate to the pyrogallol-alcohol solution the delay was increased to about 6: 1 and by addition of certain very small amounts of nitric acid to about 9: 1. Thus while the first precipitation could be observed after ten seconds in an aqueous solution of pyrogallol, it delayed until 1 ½ minute in a pyrogallol-alcohol-potassium nitrate-nitric acid solution.

As was expected the selectivity of the nerve fibre staining was found to be—within certain limits—directly proportional to the delay of the reduction.

Of course, when the precipitation is too much delayed *all* not adsorbed

argentic ions get time to be washed out from the section and there is no visible staining at all.

By a delayed reduction it is possible to obtain even the highest degree of selectivity where practically *nothing* but nerve fibres are stained (Fig. 2).

However, there are also other factors controlling the staining result. The most important of these factors seems to be the electrical charge and the size of the silver particles.

I have not been able to actually measure the charge and the size but the tint of the dispersion of the silver particles deposited in the reducing solution and the degree of the adhesion of the particles to the glass-wall of the containers I used as rough measurements.

When small amounts of a silver nitrate solution are added to a great amount of a pyrogallol-alcohol solution the silver particles remain in a very finely dispersed suspension. The tint of this suspension changes with the amount of silver nitrate added, but also with the strength of the alcohol. Using suitable amounts of silver nitrate the tint is changing from a brown or black in a strong alcohol solution to a reddish grey in a solution containing less than 60 per cent alcohol. In the last mentioned solutions the silver particles are more finely dispersed and the suspension more stable than in strong alcohol.

As the silver is less adherent to the glass-wall when deposited in a strong than in a weak alcohol solution or in pure water, the negative electrical charge of the silverparticles may be decreased by alcohol.

Proper investigations concerning the influence of different amounts of ethyl alcohol added to the pyrogallol solution revealed the remarkable fact that in series of pyrogallol solutions containing 0, 20, 30, 40, 50, 60, 70, 90 and 100 per cent alcohol there is *a very marked optimum* as to the selective staining of nerve fibres at 50—60 per cent alcohol. Stronger alcohol could be used, but the result gradually deteriorates as the concentration increases. The deterioration increases more quickly in concentrations from 50 per cent to zero.

As the viscosity of the alcohol-water mixture reaches its highest values at about the mentioned alcohol concentrations the really marvellous effect of 50—60 per cent alcohol may verify SILVER's assumption that the precipitation follows the Noyes-Nernst formula concerning the velocity of crystallization.

The process of reduction is highly sensitive as to the hydrogen ion concentration. The hydrogen ions influence the reduction rate as well as the size and the electric charge of the silver particles.

Small amounts of basic compounds added to the pyrogallol-alcohol solution, for instance pyridine, strongly accelerate the reduction. The tint of the silver suspension is a black one and scarcely any silver is deposited on the glass-wall. Hence theoretically an alkalinization of the reducing solution should act destroying on the selectivity of the nerve fibre staining and so it really does.

On the contrary, when the pyrogallol-alcohol solution is slightly acidified the

precipitation is very much delayed. The tint of the finely dispersed silver suspension is a reddish yellow and the deposition of silver on the glass-wall a greyish yellow. The selectivity of the staining is very pronounced.

The silver particles adhere to the slide where it has not been sufficiently cleaned (by the egg albumen), that is mainly to the backside of the slide, where the silver precipitates can easily be removed. In the section, however, no silver precipitates are formed presuming that the hydrogen ion concentration is properly adjusted.

Where dust particles accidentally are placed on or in a section or where other defects have caused an adsorption of argentic ions, granular or thready silver precipitates are formed. Such precipitates, however, may always be easy to identify as artefacts.

By using nitric acid added to the pyrogallol-alcohol solution not only the nerve fibres but also the blood capillaries and the reticular fibres between smooth muscular cells are stained. By addition of potassium nitrate such detrimental stainings are suppressed.

A reducer consisting of pyrogallol, alcohol, potassium nitrate and nitric aced in carefully adjusted proportions is easily destroyed by the addition of silver nitrate and should not be used more than once. As the process of staining after all takes place in the section and not in the surrounding solution it is most convenient and less expensive to add the potassium nitrate to the silver nitrate solution, which can be daily used for a long time.

3. THE TONING.

As was already stated by BIELSCHOWSKY (1902) the toning of the silver stained sections in a bath of gold chloride improves the clearness and intensity of the staining, the yellowish stain of the background changing to a very light greyish tint and the dark brown of the nerve fibres to a bright black.

By the toning the metallic silver is simply displaced by metallic gold and scarcely anything is obtained but a suitable change of the tint.

Supposing, however, the auric ions still remaining in the section are reduced by treatment with a solution of oxalic acid as for instance in the procedure introduced by BODIAN (1936) the gold stain is actually intensified in a similar way as the silver "nuclei" are "developed" by the reduction of argentic ions.

At the same time, however, the reticular fibres are stained. Hence for sections from specimens containing nerve fibres as well as non-nervous tissue elements an oxalic acid reduction of the auric ions must be avoided, presuming of course that silver nitrate and not "protargol" has been used as mordant.

On the other hand an alkaline precipitation does no harm. Hence a solution containing aniline oil (introduced for the purpose by NABIAS (1904)) in 50 per cent alcohol gives a very useful counterstaining and intensifying.

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The auric ions are much more easily reduced than are the argentic ions. Hence the reducer used for the auric ions must be very much diluted, otherwise the tint of the section becomes a bluish one as a result of the formation of numerous small, but microscopically visible, spherical gold precipitates. Only when the auric ions are *slowly* reduced the tint becomes reddish, the gold particles sufficiently finely dispersed and the staining a satisfactory one.

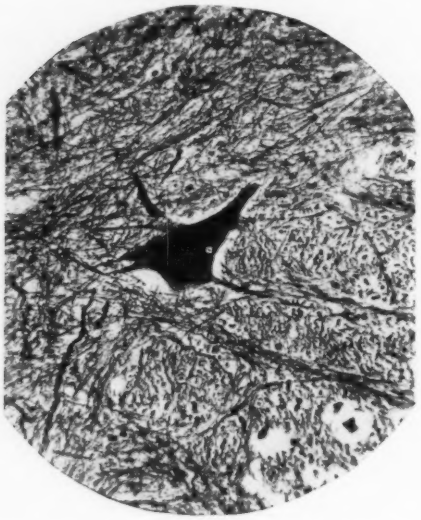

Fig. 3. Part of the ventral column of the spinal cord of Ox. Fixed in formol. Staining procedure very much simplified the spinal cord being extremely easy to stain: Mordanting for 5 minutes in 10 % silver nitrate at 20° C; reduction for 2 minutes in 1 % pyrogallol and 55 % alcohol at 25° C. Toning, but no intensifying or fixing. The section ready for examination within 15 minutes. Cell bodies red, nerve fibres black stained. Photomicrograph.

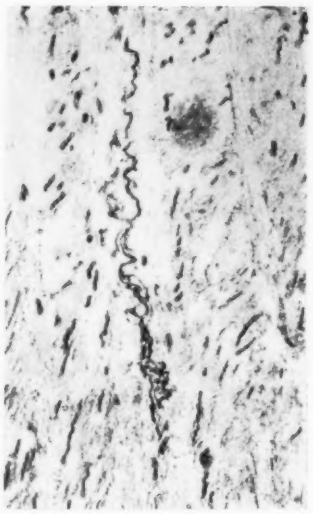

Fig. 4. Nerve fibres in the Tunica media of the Aorta, Ox, fixed in Bouin's fluid. Temperature of reducer 40° C. Photomicrograph.

For sections from parts of the central nervous system (of mammals) I sometimes found it suitable not to reduce the auric ions at all and even not to fix (Fig. 3). Within a day or two a very clear red counterstaining is obtained by a slow reduction of the auric ions still remaining in the mounted section. Generally, however, the sections should be fixed in the usual manner in a solution of 5 per cent sodium thiosulphate.

4. SUMMARY.

According to the theory advanced in this paper the silver nitrate staining of nerve fibres is depending upon two main factors: (1) the formation of nega-

tively electrically charged "germs" or "nuclei" of reduced, metallic silver (LIESEGANG 1911) and (2) the presence of positively electrically charged argentic ions, which constitute the "potential stain".

Organic matter, inclusively the proteins in fixed tissues and particularly the protein-formol compounds formed during the fixation, are able to reduce

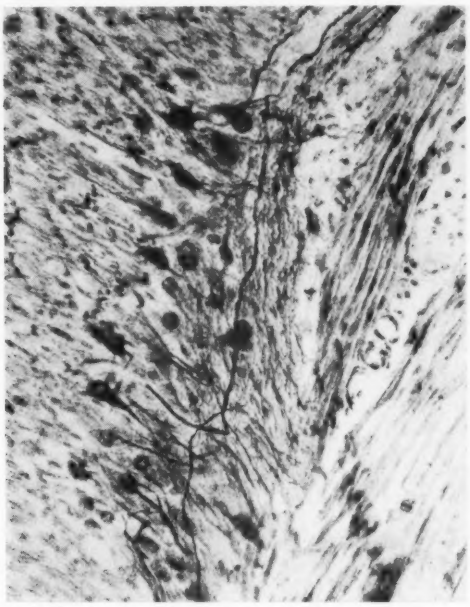

Fig. 5. Ganglion of the myenteric plexus of the small intestine of a dog, fixed in Bouin's fluid. Temperature of reducer 45° C. Silver impregnation repeated. Photomicrograph.

argentic ions even in the dark. Hence by the treatment (or mordanting) with silver nitrate silver "nuclei" are formed everywhere within the tissue structures.

During the mordanting the tissues assume a light yellow-brown tint, which is the visible effect of the formation of the silver "nuclei". The tint is most rapidly formed and most easily observable where there are great amounts of nerve fibres. Hence the "nuclei" are not uniformly distributed but preferably placed in the nerve fibres, where there may be any "argyrophilic", powerfully reducing substance. The stainability in itself is decisively depending upon such "argyrophilic" substances. The reduction-oxidation potentials of the tissue substances as well as that of the argentic ions and hence even the distribution of the "nuclei" are depending upon the hydrogen ion concentration.

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The result of the mordanting also depends upon time and temperature and, of course, upon the concentration of the argentic ions.

In a mordanted section there are not only silver "nuclei" but also still unreduced argentic ions, which are partly adsorbed to the "nuclei", partly free and uniformly distributed. When the last mentioned argentic ions are completely washed out no visible staining of nerve fibres is obtainable (supposing

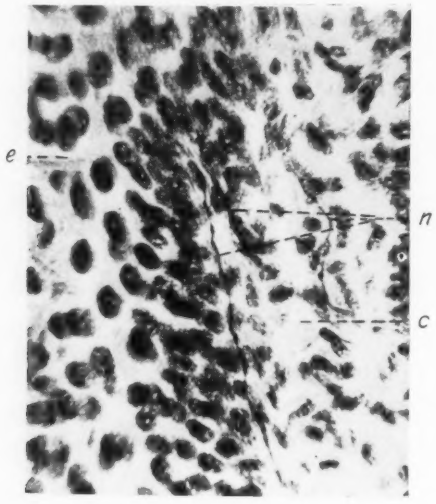

Fig. 6. Sensory nerve fibres in the stratified squamous epithelium of the tongue of a rabbit. Bouin's fixative. Double silver impregnation. Temperature of reducer 45° C. *e*, stratified squamous epithelium; *c*, subepithelial connective tissue; *n*, sensory nerve fibres. Photomicrograph.

of course that the amount of "nuclei" and hence even of the *adsorbed* argentic ions has not been increased by a prolongation of the mordanting time). Hence the free argentic ions constitute the potential stain or at least the major part of it. When the section, without previous rinsing, is transferred to a photographical developer *all* argentic ions are almost instantaneously transformed to reduced silver forming a stain wherever "nuclei" are placed and besides numerous irregular silver precipitates depositing anywhere. But when the precipitation is sufficiently *delayed* silver molecules in a *first* moment are formed *exclusively* where the "nuclei" and the adsorbed argentic ions are *particularly concentrated*, that is in the nerve fibres. In a *second* moment further argentic ions get time to be concentrated by adsorption to these "nuclei" and in a *third* moment the newly adsorbed argentic ions are transformed to silver molecules, *and so on*. Hence the 'nuclei" in the nerve fibres, acting as precipitation centres, are *growing* to a visible stain by a continuous and systematical addi-

tion of argentic ions and silver molecules. (Precipitation of this type can be observed under the microscope when a drop of a silver nitrate solution is placed on a slide and a trace of a suitable reducer (pyrogallol or pyrocatechin) is added to the drop.) By a simultaneous agitation of the slide the excess of free argentic ions is washed out prior to the delayed transformation to stain, leaving the non-nervous tissue elements unstained or only weakly counter-stained. Hence within certain limits the *selectivity* of the nerve fibre staining is directly proportional to the delay of the precipitation.

The size and the electrical charge of the silver particles, the hydrogen ion concentration and the temperature (SILVER 1942) and above all the nature and concentrations of the chemicals used for obtaining a delayed precipitation also decisively influence the selective silver nitrate staining of nerve fibres.

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B. THE PROCEDURE.

The specimens should be as fresh as possible. BOUIN'S fluid or formol (1 part of the commercial 40 per cent formol and 3 parts of distilled water) or absolute alcohol or CARNOY'S or other similar fixatives could be used, BOUIN'S being one of the most suitable. Fixatives containing osmic acid, chromic acid, potassium dichromate or mercuric chloride must not be used.

The stainability of specimens stored in alcohol for a long time may be decreased. To my experience, however, it is possible to obtain a satisfactory staining of specimens stored for many years, particularly when stored in formol.

The paraffin sections should be 5—25 microns, most suitable about 15 microns, and fixed on slides by Mayer's egg albumen.

All glass-ware and chemicals to be used *must* be chemically pure as for analysis. The slightest impurities are able to influence or destroy the staining. The silver nitrate and the pyrogallol in particular must be perfectly pure. I mostly used chemicals from Baker Chemical Co., Phillipsburg, N. J. ("Baker's Analyzed").

Heavy metals (iron forceps) and metal compounds are very deleterious and must not be brought into the silver nitrate or gold chloride solution or acid solutions used as fixatives or otherwise in the procedure.

The glass-containers used for the reducer and for rinsing must be big enough to permit a rather vigorous agitation of the slide.

It is unnecessarily to perform the staining in the dark, subdued or artificial light being harmless.

SOLUTIONS.

a. *Distilled water* from an ordinary laboratory distiller I used without re-distilling.

b. *Stock solution of nitric acid:*

1 per cent of nitric acid, either prepared by dilution of the official nitric acid and determined by titration against normal sodium hydroxide, or most conveniently ordered from a chemist's.

c. *Solution of glycine:*

Glycine (aminoacetic acid)	1 gr
Distilled water	20 cc

d. *Solution for preliminary treatment (acidifying):*

Commercial 40 per cent formol	25 cc
Distilled water	75 cc
Stock solution b.	6 drops (0.2 cc)

e. *Mordant:*

Silver nitrate	15 gr
Potassium nitrate	10 gr
Distilled water	100 cc
Solution c.	1 cc

f. *Reducer:*

Pyrogallol	10 gr
Distilled water	450 cc
Absolute ethyl alcohol	550 cc
Stock solution b.	2 cc

Note: Generally the commercial 95 per cent alcohol is not pure enough. *The portion of the reducer used each time should not be used once more.*

g. *Toning bath:*

Gold chloride (yellow)	0.5 gr
Distilled water	100 cc
Glacial acetic acid	3 drops

h. *Intensifier:*

50 per cent ethyl alcohol	100 cc
Aniline oil	2 drops

i. *Fixing bath:*

Sodium thiosulphate	5 gr
Distilled water	100 cc

THE STAINING PROCEDURE.

1. Deparaffinize and transfer to distilled water in the usual manner. Sections from specimens fixed in BOUIN's fluid should be decolorized in alcohol containing a few drops of ammonia (or by treatment for 2—3 minutes with a portion of the mordant exclusively used for this purpose and afterwards *directly transferred* to (a new portion of) the mordant, point 4. below).
2. Treat for about 5 minutes in the solution d.
3. Rinse for about 5 minutes in distilled water, successively in 3 containers.
4. Mordant for 15 minutes in the silver solution, solution e., at 20°—25° C (or for 4—5 minutes at 35° C).
5. Take up the slide, let the silver solution run off and reduce, without previous rinsing, for 1 minute in the reducer, solution f., at 30°—45° C (compare note below) agitating the slide at first rather vigorously, later more gently.
6. Rinse, agitating the slide, for about 5—10 seconds in 50 per cent ethyl alcohol.
7. Wash for about 5 minutes in distilled water, successively in 3 containers. Remove precipitates from (the backside of) the slide.
8. If necessary, repeat the procedure *from point 2.* above. (The second time the mordanting could be limited to a few minutes only and the temperature of the reduser to e.g. 30° C.)
9. Tone in the toning bath, solution g., until the light yellow-brown silver tint is faded all over (within a few minutes); examine under microscope.
10. Without rinsing, intensify and counterstain, agitating the slide, for at least 15 seconds in the intensifier, solution h. (Sections, containing nervous tissues only, should be intensified, after rinsing, in 2 per cent oxalic acid.)
11. Rinse at tap (for about 30 seconds).
12. If necessary, repeat the procedure from point 9.
13. Fix, agitating the slide, for about 5 seconds in the fixing bath, solution i.
14. Rinse at tap (for about 30 seconds).
15. Dehydrate, mount.

Note: The stainability of various specimens differs within wide limits. Therefore it may be necessary to adapt the temperature of the reducer by trials. Of course a raising of the temperature intensifies the staining and vice versa. Generally the temperature should be 40°—45° C.

As a common rule the sections should begin to assume a light yellow tint between 5 and 10 seconds past the moment of the beginning of the reduction. In sections from parts of the central nervous system, however, the tint should be observable at once.

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THE EARLY EMBRYOLOGY AND PLACENTATION OF PROCAVIA CAPENSIS

BY

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THE EARLY EMBRYOLOGY OF PROCAVIA CAPENSIS

INTRODUCTION.

A. PREVIOUS WORK ON PROCAVIA CAPENSIS.

Literature dealing with the placentation of Procavia or Hyrax dates back as far as HOME (1814), but the most comprehensive studies of recent years have been those of THURSBY-PELHAM (1924), WISLOCKI (1928, 1930) and WISLOCKI and VAN DER WESTHUYSEN (1940). In her paper Mrs. THURSBY-PELHAM summarised the views expressed in earlier papers so that it is not necessary to repeat them here. The present paper really serves to supplement the information supplied by THURSBY-PELHAM (1924) and WISLOCKI and VAN DER WESTHUYSEN (1940).

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THURSBY-PELHAM's research was based on an examination of fifteen uteri, of which "six were apparently non-pregnant and nine showed placental swellings." Of these, two of the non-pregnant uteri were described. In the pregnant uteri, the smallest uterine swelling observed was one which showed an external diameter of 8 mms., but the tissues of this specimen were not very well preserved. The investigations of Wislocki and VAN DER WESTHUYSEN were based on eleven specimens of Procavia capensis. Of these, none were at stages of development younger than the limb-bud stage.

This paper, therefore, aims at describing the condition of the uterus prior to implantation, and the embryology and placentation of stages younger than those previously described, thus partly filling the gap which at present exists in our knowledge of the development of Procavia capensis.

B. MATERIAL USED.

The material on which this investigation has been based was collected in the Graaff Reinet district of the Karroo. It consists of over 400 uteri and is the same material as that which was mentioned by Prof. C. J. VAN DER HORST in a short article published in "Science," Vol. 93, No. 2418, 1941.

In selecting material for this work the size of the uterine swellings was taken into account. The diameter of the smallest visible swelling was 5 mms. and this dilatation contained an embryo in the blastocyst stage. However, if the swelling is less than 5 mms. in diameter, then it is no larger than the diameter of the uterus itself. Therefore it becomes more difficult to locate very early stages in the uterus. I was fortunate enough to find a younger stage, the morula. This did not cause any enlargement of the uterus. It was found only after examining the condition of the corpora lutea and then sectioning the whole oviduct and uterus, bit by bit, and studying each section. Other

attempts were made in this way to find even younger stages, but without success.

The material was all fixed in Bouin and afterwards preserved in 70 % alcohol and the tissues were, on the whole, in a good state of preservation for histological study.

I did not succeed in finding the fertilized egg or an egg which had only completed the initial stages of segmentation, so that the youngest stage described is the morula. From the extensive material available, specimens were selected showing swellings with diameters of 5 mms., 6 mms., 7.2 mms., 8 mms., and so on. Thus a complete record of the early placentation and embryonic development could be made.

In addition to the uterus containing the morula, three other uteri which showed no uterine swellings have been described. These three are non-pregnant uteri.

One difficulty encountered when making a selection of embryos for description was that the relative increase in the diameter of the uterine swelling was not always an indication of a progressively later stage in embryonic development.

The following embryos have been described:

A. *Morula.* Embryo I.
No visible uterine swelling.

B. *Blastocyst.* Embryo II.
Uterine swelling diameter 5 mms.

C. *Stage of the amnio-embryonic vesicle.*
Embryo III. Uterine swelling diameter 6.5 mms.
Embryo IV. Uterine swelling diameter 7.2 mms.
Embryo V. Uterine swelling diameter 6 mms.
Embryo VI. Uterine swelling diameter 8 mms.

D. *Early primitive streak stage.* Embryo VII.
Uterine swelling diameter 8.5 mms.

E. *Later primitive streak stage.* Embryo VIII.
Uterine swelling diameter 9 mms.

PLATE I.

Fig. 1. Morula lying free in the uterine lumen. × 100.—Fig. 2. Section of the uterus showing the position of the morula in the uterine lumen. × 12.—Fig. 3. Early blastocyst showing the formation of the primary amniotic cavity. Note the first appearance of mesoderm in the segmentation cavity. × 180.—Fig. 4. Shows the destruction of the uterine epithelium by the trophoblast of the blastocyst in specimen II. Note that attachment has taken place all round the embryo. × 180.—Fig. 5. Shows the amnio-embryonic vesicle of specimen IV. Note the mitotics and cell inclusions in the ectoderm, and in the coagulum in the amnio-embryonic cavity. × 150.—Fig. 6. Shows the dislodged amnio-embryonic vesicle of specimen V. Note the elongation of the stalk region due to the proliferation of the stalk mesoderm and note also the presence of cell-inclusions. × 150.

PLATE I.

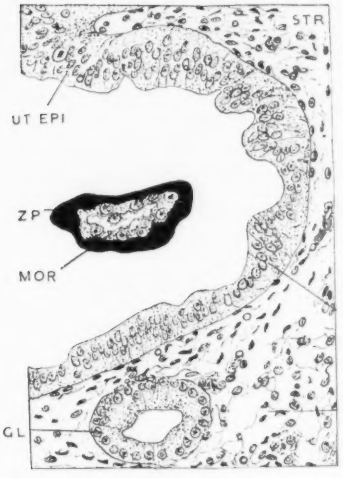

FIG. 1.

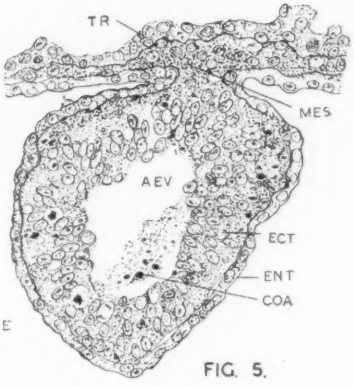

FIG. 5.

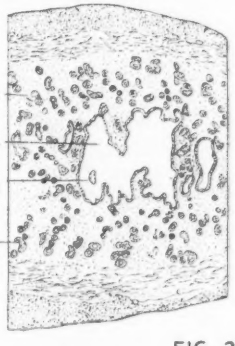

FIG. 2.

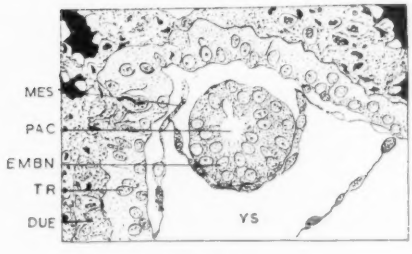

FIG. 3.

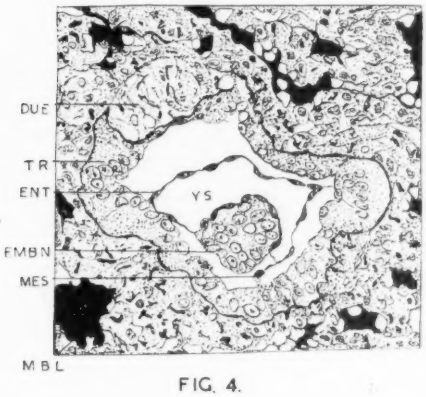

FIG. 4.

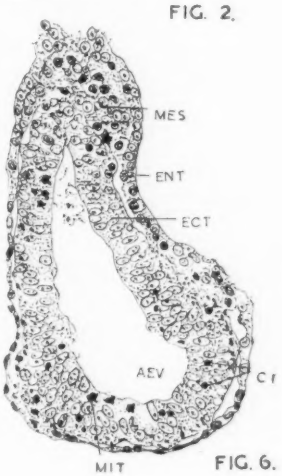

FIG. 6.

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F. *5-somites stage.* Embryo IX.
Uterine swelling diameter 10.9 mms.
G. *6—7 somites stage.* Embryo X.
Uterine swelling diameter 10.4 mms.

EARLY EMBRYOLOGY OF PROCAVIA CAPENSIS. DESCRIPTION OF EMBRYOS CLASSIFIED IN INTRODUCTION.

A. MORULA.

Embryo I.

This morula consists of about 112 cells and is 0.13 mms. × 0.17 mms. × × 0.05 mms. in size. These measurements are only approximate because the specimen is misplaced and slightly damaged in a few sections.

It is still enclosed by a thick zona pellucida and is lying completely free in the main uterine lumen (Pl. I, Figs. 1 and 2).

The cells are vacuolated and have large, oval, vesicular nuclei which are placed in the half of the cell nearest to the zona pellucida. Most nuclei have two nucleoli.

B. EARLY BLASTOCYST.

Embryo II.

The blastocyst is lying in the main uterine cavity and is attached closely on all sides to the uterine mucosa. Its implantation is, therefore, central or, to use MOSSMAN's nomenclature (1937), it is circumferential. This is true of all embryos which were examined. The orientation of the embryonic node to the uterus, however, varies considerably in the different embryos. In this specimen the orientation of the embryonic node is lateral.

The blastocyst is rather irregular in shape. It is 0.49 mms. in length measured in relation to the longitudinal axis of the uterus. Its wide diameter is 0.15 mms. and the short diameter is 0.09 mms., the last two measurements excluding the trophoblast. For comparative purposes it was found necessary to exclude the trophoblast when measuring the blastocyst, because of the very irregular nature of the outer surface of the trophoblast in the older stages.

The embryonic node measures 0.09 mms. in length and 0.07 mms. in diameter, and is oval in shape. At one point, which may be regarded as the posterior end in view of later developments, the node is connected to the trophoblast by a short and narrow stalk, consisting of six cells. These have the appearance of ectodermal cells and are continuous with the trophoblast. At the anterior end the node is separated from the trophoblast by a narrow cleft.

The nuclei of the nodal cells are large and vesicular. They are similar in appearance to those of the trophoblast. Spaces appear between a few of the nodal cells and, in two of the sections, some of these intercellular spaces have fused to form a single, larger cavity which probably represents the beginning of the primary amniotic cavity (Pl. I, Fig. 3).

The entoderm of the blastocyst is a continuous, distinct cell layer which completely surrounds the large yolk sac. In a few places the entoderm has been pulled away from the trophoblast but this is clearly an artifact. During life, the entoderm obviously lies in close contact with the trophoblast (Pl. I, Fig. 4). The cells of the entoderm are spindle-shaped with oval, chromatic nuclei. The entoderm also completely covers the embryonic node except that it does not penetrate into the cleft between the node and the trophoblast (Pl. I, Figs. 3 and 4). This cleft can be regarded as the rest of the segmentation cavity.

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A few cells are becoming dislodged from the entoderm and are penetrating into this cavity. They may represent the first mesodermal cells of the stalk.

The most striking characteristic of the trophoblast is its extremely irregular appearance. It is closely applied to the uterine mucosa at every point. Its cells are actively engaged in destroying the uterine epithelium. In fact, at this early stage, the uterine epithelium has already completely disappeared except for some small patches of tissue and a few isolated, degenerate epithelial cells (Pl. I, Figs. 3 and 4).

The irregular appearance of the trophoblast is due to the variations in the size and form of its component cells. In parts where the uterine epithelium has been totally destroyed, the trophoblast cells are tall and columnar. In other places where the epithelium has gone except for a few degenerate nuclei near the basement membrane, the trophoblast cells are cuboidal in form. Finally, in those few areas where the uterine epithelium is still uninterrupted though very disorganised, the trophoblast cells in contact with it are flatter than elsewhere and resemble squamous epithelium (Pl. I, Fig. 4). Therefore, although the trophoblast forms a distinct, well-established layer of cells and is closely applied to the uterine mucosa, it has a very irregular appearance and it is, at first, difficult to recognise it as a continuous layer of cells.

C. STAGE OF THE AMNIO-EMBRYONIC VESICLE.

Embryos III and IV.

In specimen III the uterine wall is damaged so that an accurate location of the embryonic node is not possible, but attachment is probably lateral. It is definitely not mesometrial. In specimen IV attachment is mesometrial.

Blastocyst III measures 1.24 mms. in length and is 0.55 mms. in diameter,

while blastocyst IV has a length of 2.86 mms. and a diameter of 1.6 mms. The dimensions of their amnio-embryonic vesicles are as follows:

Embryo III: length 0.15 mms., diameter 0.11 mms.

Embryo IV: length 0.42 mms., diameter 0.3 mms.

Although these two embryos vary considerably in the size of their amnio-embryonic vesicles, structurally they are very similar. A mid-sagittal reconstruction from transverse sections of the amnio-embryonic vesicle of embryo IV is given in Pl. II, Fig. 8. The amnio-embryonic vesicle is a cylindrical structure which is suspended in the yolk cavity from the trophoblast by its attachment stalk. This stalk covers 30 sections, i.e. it is 0.3 mms. wide.

The amnio-embryonic cavity, the origin of which by a fusion of intercellular spaces was described in specimen II, is now well-established. It is clear that Procavia has the "closed" method of amnion-formation, i.e. by the cavitation of the embryonic node. The amnio-embryonic cavity contains a coagulum.

The wall of the amnio-embryonic vesicle is of uniform thickness throughout and as in Elephantulus (Van der Horst 1943) "No structural difference can be seen between that half which will form the embryo proper and the other that will become the ectodermal layer of the amnion." This wall consists of an ectodermal and an entodermal layer (Pl. I, Fig. 5). The entoderm gives a smooth outline to the vesicle on the outside but the surface of the ectoderm facing the amnio-embryonic cavity is irregular due to the protrusion of many of its cells into the cavity (Pl. I, Fig. 5). However, in this series, none of these ectodermal cells were found to become detached from the wall as is the case in the macaque (Heuser and Streeter 1941) and in a few instances in Elephantulus (Van der Horst 1943).

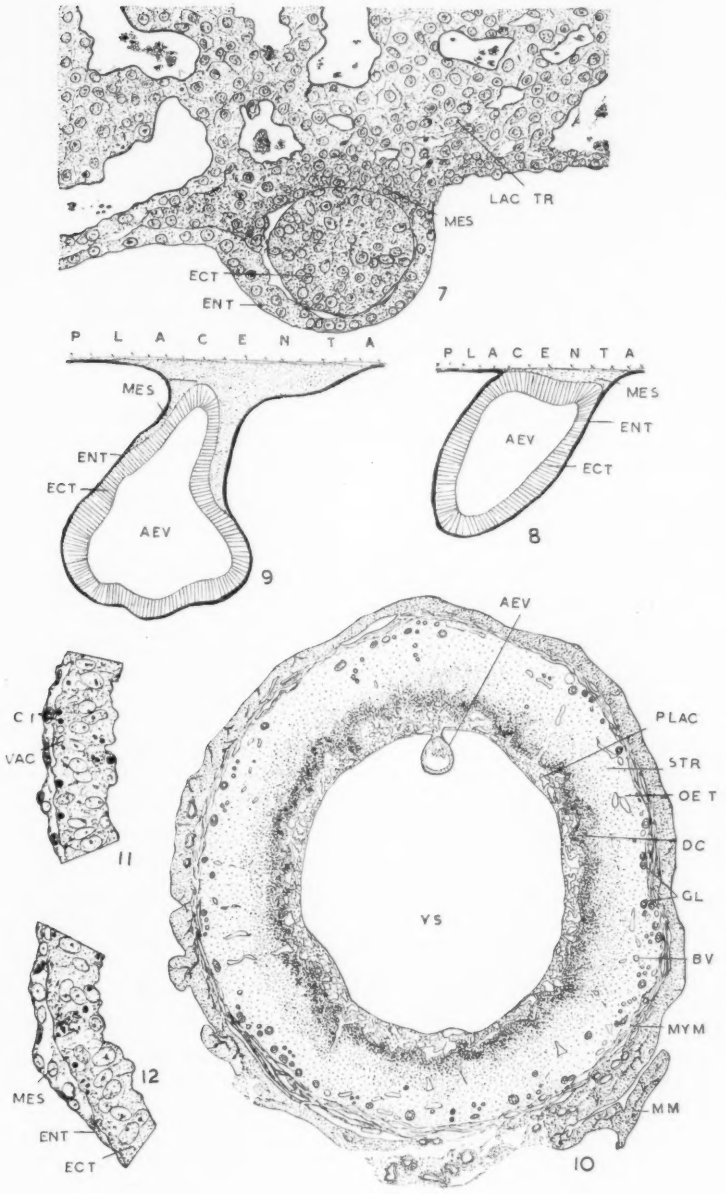
The outlines of the ectodermal cells are not clear, but their nuclei are large and many are undergoing mitosis. The positions of the nuclei in the cells vary. The cytoplasm of the ectoderm frequently contains rounded bodies of different sizes but of a uniformly deep pink colour. In some sections similar structures are lying in the coagulum of the amnio-embryonic cavity and it is assumed that they are probably of the same origin (Pl. I, Fig. 5).

PLATE II.

Fig. 7. Shows a cross-section through the stalk end of the amnio-embryonic vesicle shown in Fig. 5. Note the mesodermal cells forming the connection between the amnio-embryonic vesicle and the trophoblast. × 180.—Fig. 8. A mid-sagittal reconstruction of the amnio-embryonic vesicle of specimen IV. × 60.—Fig. 9. A mid-sagittal reconstruction of the amnio-embryonic vesicle of specimen VI. × 60.—Fig. 10. A cross-section of the uterus of specimen VI. Note the arrangement of the oedematous tissue and the presence of the decidua compacta near the trophoblast which is forming a circumferential, primordial placenta round the embryo. × 12.—Fig. 11. Shows the vacuoles and cell inclusions which are present in the ectoderm of the amnio-embryonic vesicle of specimen VI. × 240. —Fig. 12. Shows the formation of mesoderm from the entoderm of the amnio-embryonic vesicle in specimen VI. × 240.

THE EARLY EMBRYOLOGY OF PROCAVIA CAPENSIS

PLATE II.



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HILL and TRIBE (1924), in describing the embryonal ectodermal cells of blastocyst 37 of the cat, mention that "the cells contain numbers of fair-sized fat globules." In the early blastocyst, number 45 of Loris, HILL also found intracellular vacuoles which during life he believed to be occupied by fat globules (HILL 1932). It is difficult to say whether the cytoplasmic inclusions observed in these blastocysts of Procavia are of a fatty nature, and whether they can be compared with the fat globules described by HILL. The fact, however, that, in Procavia, bodies similar in form and staining reaction to those in the ectodermal cells are also found in the amnio-embryonic cavity suggests that the inclusions are of a lipo-protein nature. Similar cell inclusions are found in specimens V and VI. In the latter embryos there are also small vacuoles in some of the ectodermal cells, (Pl. II, Fig. 11), which may be occupied during life by fat globules, as suggested by HILL (1924, 1932).

A striking feature of specimens III and IV is that the ectodermal link between the trophoblast and the embryonic node described in embryo II has been lost. At no point in the attachment stalk does the ectoderm of the amnio-embryonic vesicle come in contact with the trophoblast (Pl. II, Fig. 7). Instead, the connection between amnio-embryonic vesicle and trophoblast in specimens III and IV is formed by mesodermal cells. These may have been derived from the few cells described as mesoderm, which were found in the cleft between the embryonic node and trophoblast of embryo II. In embryos III and IV this open cleft which was found in embryo II has disappeared and its place is occupied by mesodermal cells. Nevertheless, attachment is still by means of a stalk, because the amnio-embryonic vesicle is much larger than the original node and protrudes into the yolk-cavity obliquely in an anterior direction.

A few of these mesodermal cells have begun to penetrate between the trophoblast and extra-embryonic entoderm, but there are, as yet, no mesodermal cells lying between the ectoderm and entoderm of the amnio-embryonic vesicle (Pl. I, Fig. 5).

The bilaminar yolk sac continues to occupy the whole of the uterine lumen.

Embryos V and VI.

The implantation of both these blastocysts is central as in those previously described. The orientation of the embryonic disc to the uterus is lateral in embryo V but antimesometrial in specimen VI (Pl. II, Fig. 10).

Although the diameters of the uterine swellings of embryos V and VI are 6 mms. and 8 mms. respectively, the general structure and distribution of the tissues is similar in both specimens. The blastocyst of specimen V is 2.8 mms. long and 1.56 mms. in diameter, and its amnio-embryonic vesicle measures 0.32 mms. × 0.32 mms. Blastocyst VI is 4.1 mms. in length and 3 mms. in

diameter and its amnio-embryonic vesicle measures 0.48 mms. in length and 0.39 mms. in diameter.

The amnio-embryonic vesicle of embryo V has become dislodged from the trophoblast, so that the following description refers mainly to specimen VI, of which a mid-sagittal reconstruction is given in Pl. II, Fig. 9.

The attachment stalk has broadened considerably. It now covers 60 sections and is 0.6 mms. wide as compared with the width of 0.3 mms. in specimen IV. This enlargement is due mainly to the active proliferation of the mesodermal cells in the stalk, which can be seen in both embryos (Pl. I, Fig. 6, and Pl. III, Fig. 13). As in specimen IV, the ectoderm of the amnio-embryonic vesicle is widely separated from the trophoblast by mesoderm (Pl. II, Fig. 9).

At the posterior end of the amnio-embryonic vesicle particularly this stalk mesoderm is pushing between the trophoblast and extra-embryonic entoderm. Mesoderm is also penetrating on each side between the ectoderm and entoderm of the amnio-embryonic vesicle for a short distance. This mesoderm is continuous with the stalk mesoderm (Pl. III, Fig. 13) from which it probably originates. In addition, in specimen VI a few mesodermal cells can be seen between the ectoderm and entoderm in the region where the amnio-embryonic vesicle protrudes deepest into the yolk-sac. These cells do not have their origin from the stalk, being separated from it by an area in which ectoderm and entoderm are closely apposed to one another. They can be seen becoming detached from the entoderm (Pl. II, Fig. 12) and are clearly of entodermal origin. A similar method of mesoderm formation has been described in Elephantulus (Van der Horst 1943).

It is interesting to note, therefore, that in Procavia capensis proliferation of the mesoderm has taken place prior to the formation of a primitive streak.

The shape of the amnio-embryonic vesicle is no longer regularly cylindrical as in embryo IV (Pl. II, Fig. 8). The amnio-embryonic cavity is now wider near the free end of the vesicle which hangs in the yolk-sac (Pl. II, Fig. 9).

There is still no appreciable difference in the width of the ectoderm at the two poles, which would be indicative of a distinction between amniotic and embryonic ectoderm. However, due probably to the enlargement of the amnio-embryonic cavity, the thickness of the wall of the vesicle, especially in specimen VI, has become reduced. The ectodermal cells are rather tall and narrow. They have vesicular nuclei which tend to occupy the centre, or free end of the cell, nearest to the amnio-embryonic cavity. Each nucleus is about a third of the size of the whole cell.

The outer edge of the ectoderm is smooth but the inner surface is irregular as in specimens III and IV. It was noticed, however, that some of the protruding cells described in these last two embryos, did become dislodged into the amnio-embryonic cavity of embryo VI. These loose cells remain in the

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cavity where they are mixed with the coagulum which still persists in this stage of development.

Present, especially in those parts of the ectodermal cells furthest from the amnio-embryonic cavity, are numbers of intracellular inclusions and some small vacuoles (Pl. II, Figs. 11 and 12), such as were described in embryo IV.

The nuclei of the entodermal cells are small. They appear oval and vesicular when seen in flat, surface view, but are dark and pycnotic if they are turned on their edges. They are, therefore, disc-shaped.

D. EARLY PRIMITIVE STREAK STAGE.

Embryo VII.

Unfortunately, this specimen is not in a good state of preservation for histological study. As it is the first to show primitive streak formation it deserves comment in regard to the arrangement of the tissues.

Orientation of the amnio-embryonic vesicle to the uterus is mesometrial in this specimen.

The blastocyst measures 4.34 mms. in length and 3.4 mms. in diameter. The amnio-embryonic vesicle is still a more or less cylindrical sac. It has, however, elongated and is 0.79 mms. long. It has a diameter of 0.42 mms. Whereas the transverse diameter of the amnio-embryonic vesicle of embryo VII is only 0.03 mms. greater than that of embryo VI, in length that of embryo VII shows an increase of 0.31 mms. when compared with specimen VI.

The roof of the amnio-embryonic vesicle is now definitely thinner than the floor, so that amniotic and embryonic ectoderm are differentiated. The amniotic mesoderm, however, does not yet occur as a distinct cell layer.

The most striking feature of this blastocyst is that the amnio-embryonic vesicle now has neither ectodermal contact with the trophoblast as in blastocyst II, nor mesodermal attachment as in specimens III, IV, V and VI. The only tissue which retains its connection with the trophoblast is the yolk entoderm. This is due to the fact that the amnio-embryonic vesicle of blastocyst VII has been pushed away from the trophoblast by a coagulated mass which is spread

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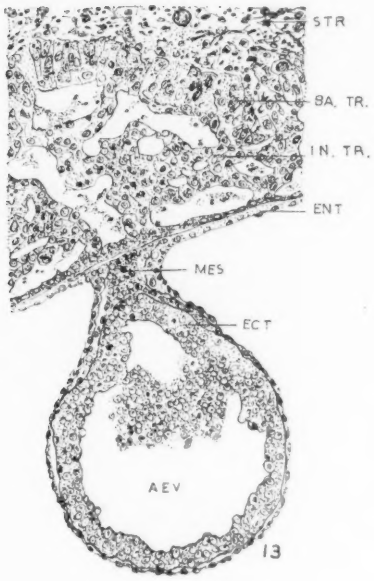
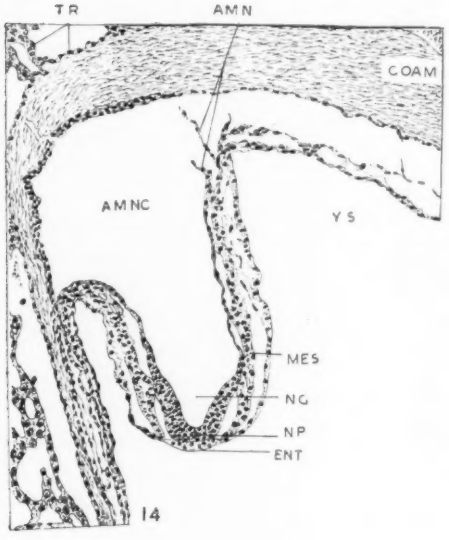
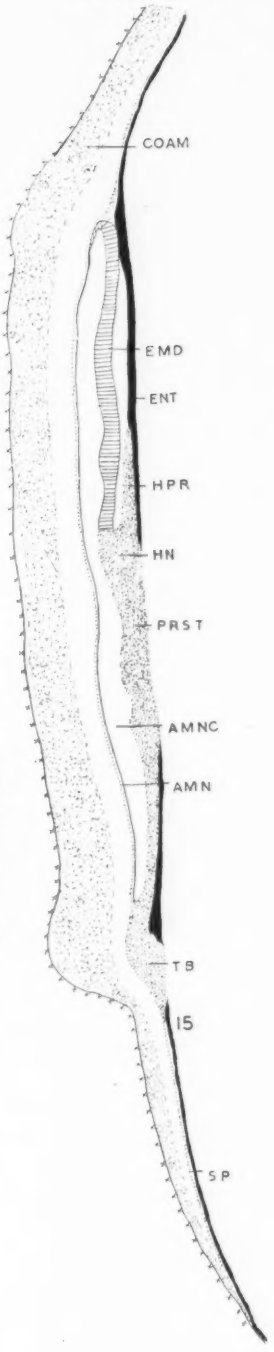
PLATE III.

Fig. 13. Shows the amnio-embryonic vesicle of specimen VI. Note the formation of mesoderm in the attachment stalk and the penetration of some mesodermal cells between the ectoderm and the entoderm of the amnio-embryonic vesicle. × 90.—Fig. 14. A cross-section of the 5-somites embryo. Note the coagulated mass which covers the embryonic pole and the thickening of the entoderm below the neural plate. × 60.—Fig. 15. A mid-sagittal reconstruction of the embryo proper of specimen VIII. Note that the splanchnic mesoderm is applied to the yolk entoderm only as far as the point of contact between the entoderm and trophoblast. The amnion is separated from the trophoblast by the coagulated mass. × 60.

PLATE III.







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out to form a wide arch over the whole of the embryonic pole of the blastocyst. This coagulum is a persistent feature of this and the later stages described in this paper. It is assumed, therefore, that it plays an important role in the development of Procavia.

In some places the amnio-embryonic vesicle is separated from the coagulated mass by a clear space. A study of this and later stages has, however, shown clearly that it is merely an artifact. Somatic mesoderm has not yet been differentiated so that the space occupied by the coagulum cannot be regarded as extra-embryonic coelom.

The mesoderm which previously formed the attachment with the trophoblast is rather damaged, but it is obvious that it has increased in dimensions. There is a greater proliferation of this tissue between trophoblast and extra-embryonic entoderm but it still does not extend beyond the point of contact of trophoblast and entoderm at the edges of the coagulated mass. This mesoderm is, therefore, completely separated from the trophoblast by the coagulum.

The mesoderm which develops between the ectoderm and entoderm of the amnio-embryonic vesicle and the initial growth of which was described in embryo VI, has also advanced. It now forms a continuous layer except at the anterior end of the amnio-embryonic vesicle which protrudes deepest into the yolk-sac.

The primitive streak occupies 15 sections near the caudal end of the amnio-embryonic vesicle. In the five sections immediately in front of these 15 sections, there has been a proliferation of the tissues to form a knot of cells which bulges into the amnio-embryonic cavity. Owing to the bad state of preservation of the tissues, it is impossible to determine whether this dilation consists only of ectodermal cells, or whether it is made up of mesoderm and ectoderm. However, its size and position in front of the primitive streak indicate that it may represent the head process which becomes well-established in embryo VIII. A blastoporal groove is present in the primitive streak.

E. LATER PRIMITIVE STREAK STAGE

Embryo VIII.

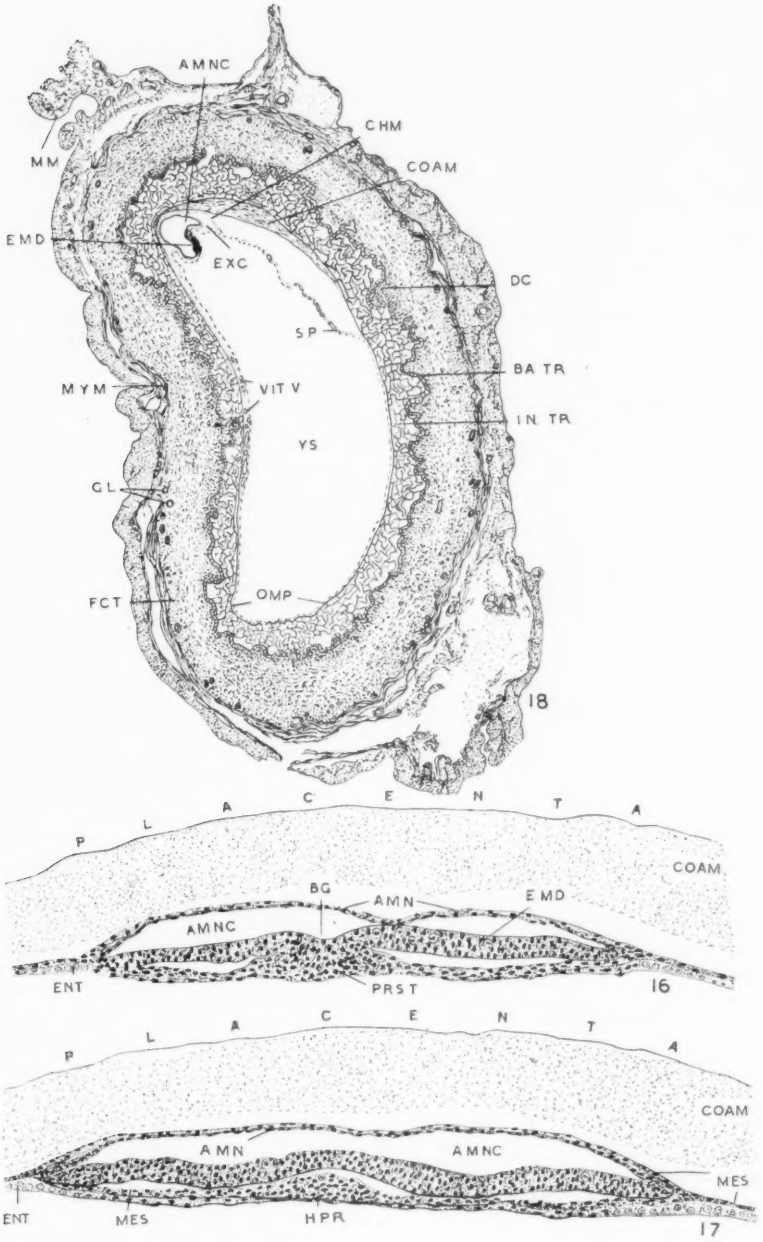
The orientation of the embryonic disc to the uterus in this specimen is mesometrial as in blastocyst IV.

PLATE IV.

Fig. 16. A cross-section through the primitive streak area of specimen VIII. Note the blastoporal groove and the coagulated mass. × 90.—Fig. 17. Shows a section through the head process of the same embryo (VIII). × 90.—Fig. 18. A cross-section of the uterus containing the 5-somites embryo. Note the formation of the exocoelom, the first appearance of the chorionic mesoderm, the presence of the vitelline vessels in the splanchnopleure and the circumferential arrangement of the primordial placenta. × 12.

THE EARLY EMBRYOLOGY OF PROCAVIA CAPENSIS

PLATE IV



The embryonic disc has flattened considerably. It measures 1.82 mms. in length and is 1.0 mms. wide. The whole blastocyst, exclusive of its trophoblast, is 5.57 mms. long and 4.25 mms. in diameter. A mid-sagittal reconstruction of the embryonic disc is given in Pl. III, Fig. 15.

The amniotic cavity is narrow and extends over the upper surface of the embryo. The mesoderm of the amnion is complete and with the amniotic ectoderm forms a thin roof to the amniotic cavity.

The mesoderm, adjoining the yolk-sac, stretches only for a short distance from the edges of the embryonic disc. This splanchnic mesoderm is still continuous with the amniotic mesoderm but is applied to the yolk entoderm only as far as the point of contact between the entoderm and trophoblast (Pl. III, Fig. 15). There is no trace of chorionic mesoderm and, therefore, no extra-embryonic coelom.

The coagulated mass described in the previous specimen continues to separate the amnion from the trophoblast.

The primitive streak is well-established and is 1.12 mms. long. At its anterior end it is slightly thickened to form HENSEN's node (Pl. III, Fig. 15). Passing forwards from this is the head process (Pl. IV, Fig. 17). In front of Hensen's node the differentiation of the neural plate is taking place but the notochord does not appear. Posteriorly, the primitive streak is narrow but finally dilates to form a tail-bud from which a narrow plate of mesoderm passes back with the extra-embryonic entoderm to form the beginning of the splanchnopleure. The entoderm is thickened for a short distance at the edge of the disc (Pl. IV, Figs. 16 and 17).

There is no blastoporal opening but there is a primitive groove (Pl. IV, Fig. 16). This occurs as a distinct depression in the primitive streak for at least fifty sections. Its exact length cannot be measured because posteriorly this furrow gradually gets shallower and shallower and finally fades away.

F. 5-SOMITES STAGE.

Embryo IX.

Orientation of the embryonic disc to the uterus is mesometrial.

The arrangement of the membranes and position of the embryo is probably a little distorted here due to the collapse of the uterine wall while embedding the specimen.

The length of the embryonic plate is 3.8 mms. and its width is approximately 1.63 mms. The blastocyst is 9.26 mms. long. Due to distortion, a single accurate measurement of the diameter is not possible. In its collapsed state, the long diameter of the blastocyst is 5.0 mms. and the short diameter is 1.75 mms.

The amnion continues to be separated from the trophoblast by the coagulated

mass, which seems to reach its maximum dimensions at this stage (Pl. III, Fig. 14).

Further mesodermal development has now taken place. A small extra-embryonic coelom has appeared which is more conspicuous at the anterior and posterior ends of the embryo than in the middle. The chorionic mesoderm, however, is present only in the region of the embryo proper and does not extend laterally to the same extent as the splanchnic mesoderm (Pl. IV, Fig. 18, Pl. V, Fig. 19). It is a striking fact that this chorionic mesoderm develops on the inside of the coagulated mass. In the midline, therefore, the chorionic mesoderm is lying close to the amnion and not to the trophoblast.

Splanchnic mesoderm continues to differentiate and has now spread round the yolk-sac to a greater extent than in specimen VIII. Nevertheless, it is still far from the abembryonic pole of the yolk-sac. Here the omphalopleure consists only of lacunar trophoblast and flattened entodermal cells (Pl. IV, Fig. 18), for neither splanchnic nor chorionic mesoderm has reached this area.

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The yolk-sac remains a large structure and is becoming vascularised in the regions on either side of the embryo proper, where splanchnic mesoderm is differentiated. There is still no development of the allantois.

Anteriorly the neural plate has broadened to form a brain plate but there is, as yet, no indication of the chiasmatic ridge or optic vesicles of the 6—7 somites stage. The neural folds and groove are visible in the region where the somites occur. Placed more posteriorly is the primitive streak which has become shorter and occupies only 87 sections. A blastoporal groove appears in only a few sections. It is not so clearly defined as in the primitive streak of embryo VIII.

Anterior to the primitive streak the entoderm is noticeably thickened below the neural plate (Pl. III, Fig. 14).

G. 6—7 SOMITES STAGE.

Embryo X.

Orientation of this embryonic disc to the uterus is antimesometrial.

The dimensions of the embryonic disc are 2.72 mms. × 2.42 mms. The length of the whole blastocyst is 9.73 mms., but its diameter could not be measured owing to the collapsed state of its wall.

A wax model of this embryo was constructed, a study of which yielded some interesting information. An unusual feature of this specimen is that the embryo seems to be twisted away from the normal longitudinal axis (Pl. V, Fig. 20). Thus it exhibits torsion as well as the normal flexion.

It is difficult to relate the development of this embryo to that of the 5-somites one, for in some respects it is more advanced and in others does not seem to have progressed as far as the 5-somites embryo. For instance, in embryo X the mesoderm of the chorion has not differentiated as fully, nor has the extra-

embryonic coelom developed to the same extent at the anterior and posterior ends, as in embryo IX. The embryonic disc of specimen X is shorter but wider than of specimen IX.

On the other hand it is more advanced in the following ways:

1. There are 6—7 somites.
2. The primitive streak is but 0.58 mms. long and the only indication of a blastoporal groove is a slight depression covering four sections (Pl. V, Figs. 20 and 23).
3. The neural groove is deeper and the neural folds are beginning to lift up from the surface.
4. Anteriorly, the brain plate has become differentiated. Although it is still only a flat plate, it is definitely more advanced in its development than that of the 5-somites embryo. At the anterior extremity are two rounded fields where the neural plate is thickened, each of which is 0.5 mms. in diameter. From the lower surface of these, the two optic vesicles can be seen developing (Pl. V, Fig. 22). These circular, raised fields are connected by a groove, the floor of which is formed by the thinner part of the neural plate. The anterior limit of the floor plate could not be determined. The groove is terminated anteriorly by a distinct ridge which also connects the two areas. This probably represents the chiasmatic ridge (Pl. V, Figs. 20, 21). It bears a striking resemblance to the optic chiasma which KINGSBURY (1922) found occupying the cephalic border of the brain plate in Squalus acanthias and which he also suggested occurred in the 4-somites cat embryo described by SCHULTE and TILNEY (1915).

DISCUSSION.

IMPLANTATION.

BONNET recognised three methods of implantation based on the position of the blastocyst attached in the uterus. These he called the central, eccentric and interstitial types. In the first method, which has been reported in the Ungulates, Carnivora, Lower Primates, some Insectivora, e.g. Hemicentetes, and in the

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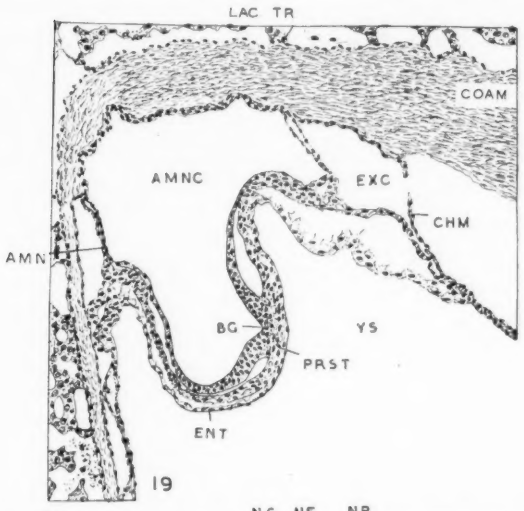
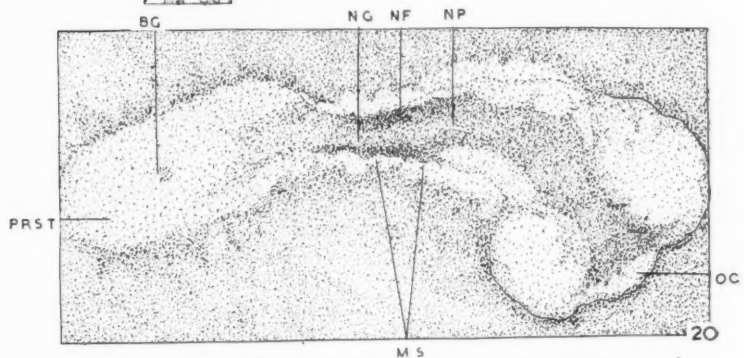
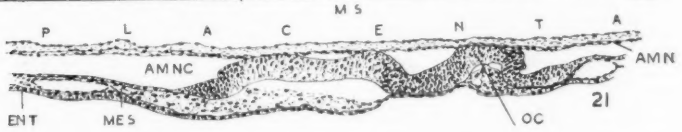
PLATE V.

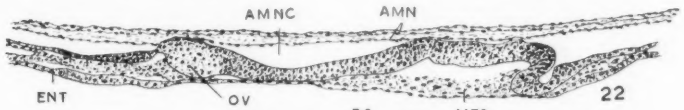
Fig. 19. Shows the same embryo as in Fig. 18. × 60.—Fig. 20. Shows the structure of the embryo of specimen X as drawn from a wax model. Note the curved position of the embryo and the two raised fields joined by the chiasmatic ridge at its anterior end, the deep neural groove, distinct neural folds and the small blastoporal groove. × 30. —Fig. 21. A section cut through the chiasmatic ridge of specimen X. × 60.—Fig. 22. A section cut through the anterior end of the embryo of specimen X to show the formation of one optic vesicle. × 60.—Fig. 23. A section through the primitive streak of specimen X. × 90.

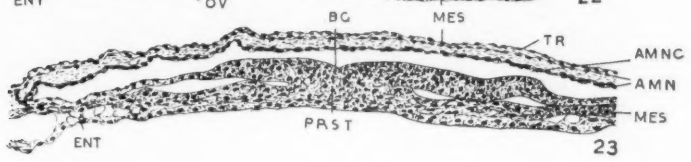
PLATE V.











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Rabbit, which belongs to the Rodentia, the ovum is lying in the main uterine cavity and is attached only superficially to the uterine wall. During its development, the blastocyst comes in contact on all sides with the uterine wall. In the eccentric type of implantation found in some Insectivora, e.g. Hedgehog, and in the Muridae, the ovum lies in a diverticulum of the uterine lumen. This furrow becomes closed off from the main uterine cavity and the coalescence results in the formation of a decidua capsularis over the embryo. The interstitial method is found in the Guinea Pig and in Geomys and occurs also in man. In this type, the blastocyst destroys the uterine epithelium and subepithelial tissue and burrows completely into the uterine mucosa. Its point of entrance is later closed by the formation of a decidua capsularis.

MOSSMAN (1937) has, however, given more specific terms for describing implantation phenomena, both in regard to the initial attachment of the blastocyst to the uterus and in regard to the orientation of the embryonic disc. He has taken into consideration not only the position of the embryo in the uterus but also its relationship to the type of placenta which is formed. He believed, therefore, that there is more to the question of implantation than can be indicated by the three terms—central, eccentric, and interstitial. For instance, he introduced the terms abembryonic, para-embryonic and practically embryonic for describing "the position of the inner cell-mass and later embryonic disc with reference to the part of the trophoblast which actively engages in the attachment process."

In describing implantation, therefore, according to MOSSMAN the following facts must be taken into consideration.

1. The orientation of the first area of attachment. This he described as antimesometrial, mesometrial or lateral. In this connection GOETZ (1937) substituted the term orthomesometrial for lateral.
2. The position of the inner cell-mass with reference to the part of the trophoblast which actively engages in the attachment process. Here he differentiated three types—abembryonic as in Rodents, para-embryonic as in the Ferret and Tree-Shrew and practically embryonic as in Galeopithecus, the Hedgehog and Macacus.
3. Variations in the depth of implantation, i.e. superficial, partly interstitial, and nearly or completely interstitial.
4. The orientation of the embryonic disc to the uterus. This he again described as antimesometrial, mesometrial or lateral.

Finally, for those types, e.g. Manis, Cetacea, Proboscidea in which first attachment to the uterus occurs all round, he used the term circumferential and qualified this by mentioning that in such types the depth of implantation is necessarily superficial. In Fig. 4 MOSSMAN (1937) placed the Hyracoidea, to which Procavia belongs, among the circumferential types as regards the region of first attachment to the uterus. He described the orientation of the embryonic

disc to the uterus as antimesometrial, although in Table 3 he indicated that there was some doubt about this, and in the caption to Plate 22 said the implantation of Procavia was unknown.

According to the nomenclature of Bonnet, the implantation of Procavia capensis is central, for the blastocyst is lying in the main uterine cavity. However, if one accepts MOSSMAN'S wider interpretations, it can better be described as circumferential in regard to its initial attachment. Nevertheless, it is definitely not a superficial attachment, for even in the youngest blastocyst here described, i.e. embryo II, the uterine epithelium at least has been destroyed practically all round. Unlike Hemicentetes (GOETZ 1937) in which animal, although implantation is central, only a small area of the trophoblast shows histolytic properties, in Procavia the entire surface of the trophoblast shows the ability to destroy and resorb the maternal tissues. In this respect Procavia resembles the Hedgehog and Man. So regular is the depth to which the trophoblast in Procavia penetrates the mucosa and so uniform is the width of the outer layer of trophoblast which consists of deep columnar cells, that a cursory examination might easily result in this layer being taken to represent the uterine epithelium. In such a case a superficial resemblance to types like Sus, Ovis, and Loris would be understandable, for in these cases implantation is circumferential but is also superficial. Procavia must instead be regarded as rather exceptional for, although the original attachment to the uterus is circumferential, it is definitely not superficial. Moreover, the entire trophoblast takes part in the destruction of the uterine tissues and, therefore, the terms abembryonic, para-embryonic, etc., are not applicable to this animal.

With regard to the orientation of the embryonic disc towards the uterus, Procavia is also of interest. As mentioned earlier, MOSSMAN (1937) suggested this orientation might be antimesometrial. Of the nine embryos described in this paper, four are mesometrial, two are antimesometrial, two are lateral and one cannot be accurately placed. Therefore, in this respect Procavia must be regarded as irregular. It seems to be a matter of chance as to whether the embryonic disc is orientated mesometrially, antimesometrially or laterally. It is possible that this haphazard method of orientation of the embryonic discs is linked up with the form of the placenta produced by this animal. The early placenta is circumferential and, therefore, the association of the developing embryo with the uterus will be the same at any point of attachment.

It is highly probable that, as more data become available regarding the implantation of animals which have the circumferential type of attachment, the variability of the orientation of the embryonic disc will be found to be a feature which is generally associated with this circumferential method of implantation. According to present knowledge, it is obvious from descriptions of the orientation of the embryonic disc in animals like Manis, Canis, Sus, Ovis, and Putorius, all of which show circumferential implantation, that difficulties and

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queries still exist, and that exact information has still to be obtained. This was shown clearly in MOSSMAN's descriptions of the plates in his paper on the "Comparative morphogenesis of the Fetal Membranes" (1937). For instance, the implantation of Canis familiaris was described as "Circumferential and superficial with disc usually turned antimesometrially but occasionally irregularly lateral," while that of Ovis was "circumferential and superficial. Probably antimesometrial orientation of the disc." The arrangement of the disc in Manis was given as "probably antimesometrial," of the cat as "antimesometrial to irregular" and of Sus as "antimesometrial (?)." All these descriptions support the view that a more detailed study of the implantation of animals like those mentioned above, as well as those like Equus, the Proboscidea and Sirenia, about which we have as yet no information regarding implantation, may show a definite relationship between the circumferential, initial attachment and the haphazard orientation of the embryonic disc. On the other hand, it must be remembered that a few cases have been described, e.g. Nyctinomus cynocephalus in which, although implantation is circumferential, the orientation of the embryonic disc can definitely be given as antimesometrial.

AMNIOGENESIS.

Amnion formation in Procavia is of the "closed" type, achieved by cavitation as shown in Pl. I, Fig. 3. It shows, moreover, a broad resemblance to that of such varied forms as the Hedgehog, Galeopithecus, Hemicentetes, and some Primates.

The Procavia embryo II shows that amnion formation is initiated by the appearance of a few inter-cellular spaces in the embryonic node, as in Hemicentetes (GOETZ 1937). These spaces later fuse to form a single, central cavity which has been termed a primary amnio-embryonic cavity. This central cavity remains completely surrounded by ectoblast.

I am in agreement with GOETZ (1937) who said of Hemicentetes "Bei der Entstehung der Intercellularlücken im Inneren des Embryonalknotens, d. h. in den frühesten Stadien der Archamnion-bildung von Hemicentetes scheint die Saftabgabe im Vordergrund zu stehen, wenn sie nicht sogar als einziger Faktor die Schizocoelie hervorbringt." In the earliest stages of Procavia there are no indications of the operation of cytolytic processes or the fragmentation of cells, so that it is highly probable that secretion is mainly responsible for the initial formation of the primary amnio-embryonic cavity in this animal as well. Several earlier workers in the field of amniogenesis have shown that the subsequent increase in the size of amnio-embryonic cavity or archamnion is also assisted by the disintegration of cells. Evidence for this was found in the presence of cell fragments in the amnio-embryonic cavity. Such fragmentation has been described by CARAZZI (1918) in the Guinea Pig, by

HUBRECHT (1919) in Galeopithecus, by DA COSTA (1920) in Miniopterus, and by KOHLBRUGGE (1913) in Xantharpya. Similar evidence has now been found in Procavia, for particularly in embryos V and VI can cell fragments be seen lying with some coagulum in the amnio-embryonic cavity.

GOETZ (1937) summarized very comprehensively the various methods by which the primary amniotic cavity may originate so that there is no need to recapitulate this work here. It is, however, worthwhile to mention that in Procavia it is quite clear that the original cavity forms inside the embryonic node and in all the early stages remains completely enclosed by the ectoblast of the node. There is no question of the possibility of the formation of a false archamnion between the trophoblast and the embryonic node such as was described in the Muridae, in Vespertilio (VAN BENEDEN 1899), and in Miniopterus (DA COSTA 1920). In addition to the separation of the amnio-embryonic cavity from the trophoblast by ectoderm in all the Procavia embryos described in this paper, there is also an early interposition of mesoderm between the trophoblast and the ectoderm of the amnio-embryonic vesicle. Moreover, in the somewhat older embryos VII, VIII, IX and X the amnio-embryonic vesicle is pushed away from the trophoblast by a mass of coagulum.

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GOETZ (1937) pointed out that in most cases where the extra-embryonic mesoderm differentiates early the original archamnion, or primary amnio-embryonic cavity becomes the real amniotic cavity of later stages. This he proved to be true of Hemicentetes. However, in this animal GOETZ showed that the archamnion, although at first in the centre of the node, later becomes eccentrically placed. In Procavia, on the other hand, the cavity remains central in position until the flattening out of the vesicle takes place as in embryo VIII. Nevertheless, in Procavia it is also the whole of the amnio-embryonic cavity which becomes the real amniotic cavity, a two-layered amnion being produced by the early penetration of extra-embryonic mesoderm. The ectoderm of the amnion is obviously formed by the narrowing down of some of the original ectodermal cells of the amnio-embryonic vesicle as in Hemicentetes (GOETZ 1937) and not by delamination from the trophoblast as described by HUBRECHT in his work on the Hedgehog.

The shape and position of the amnio-embryonic cavity and, in fact, of the whole vesicle in Procavia bears a striking resemblance to that of Galeopithecus (HUBRECHT 1919). This is most noticeable, for instance, if one compares the Galeopithecus blastocyst, No. 6, of HUBRECHT with that of embryos III or IV of Procavia described in this paper. Not only does amniogenesis occur in the same way, but the manner in which the amnio-embryonic vesicle protrudes at its anterior end into the yolk-sac, and the initial formation of mesoderm in the posterior stalk region seem to be identical.

YOLK-SAC AND ENTODERM.

Although it is not possible to give precise information in regard to the origin of the yolk-sac and entoderm, because even in the earliest blastocyst of Procavia described in this paper the yolk-sac entoderm is already a continuous layer of cells, it seems fairly certain that the yolk-sac is formed in the same way as in most mammals. In these animals the yolk-sac is produced by the gradual spreading of entoderm round the inner surface of the trophoblastic shell. In the stages of Procavia described in this paper even the early blastocyst shows the first indications of an amnio-embryonic cavity. Although the entoderm of the yolk-sac has shrunk away from the trophoblast in some places, the fact that it has maintained contact at several points, indicates that the shrinkage has been due to the fixation process.

Just as the method of formation of the yolk-sac in Procavia must be left largely to speculation owing to its already completed form in the material available, so also is it impossible to give an account of the origin of the entoderm, which in the earliest embryo here described is already a continuous layer of cells. It is difficult, therefore, to say wether this tissue has arisen by delamination of cells from the lower border of the embryonic node, which is the more generally accepted method, or whether it arises "through a migration of entodermal mothercells from among the embryonic ectodermal cells of the inner cell-mass," such migrating cells subsequently forming a continuous layer on the under surface of the node. This last type was shown to occur in Tatusia (PATTERSON 1913).

CONNECTING STALK AND MESODERM.

From the earliest blastocyst stage up to the time of the first appearance of the primitive streak in the amnio-embryonic vesicle, the early embryonic cylinder of Procavia is connected at its posterior end with the trophoblast. Such a connecting stalk is also characteristic of all Primates, except the Lemuroidea, of Elephantulus and of Galeopithecus. However, as VAN DER HORST (1943) pointed out, the connecting stalk of Elephantulus does not show the typical structure of that founded in the other animals mentioned above.

Procavia, on the other hand, bears a striking resemblance to Galeopithecus with regard to the development, structure, and final behaviour of its connecting stalk. HUBRECHT (1919) pointed out that in Galeopithecus "Im Anfang ist eine ektodermale Verbindung zwischen Trophoderm und Embryonalknoten anwesend. Dieser Haftstiel wird später mesodermal und weist Gefässe auf, welche mit denen der Splanchnopleura des Dottersacks in Verbindung treten. Noch später verästelt sich dieser Haftstiel und geht schliesslich zu Grunde." In

Procavia there is also at first an ectodermal connection between the embryonic node and the trophoblast but this is later replaced by mesoderm which proliferates rapidly and causes the extension of the stalk in a caudal direction. However, in Procavia this mesoderm never becomes vascularized nor does the stalk become branched.

In both Galeopithecus and Procavia the connecting stalk is of a temporary nature. In Galeopithecus the mesoderm is split into chorionic and amniotic mesoderm by the comparatively early appearance of the exocoelom which separates the embryo proper from the trophoblast. In Procavia, the severance of the connection between amnio-embryonic vesicle and trophoblast is brought about in a different way. There is interpolated between the mesoderm of the stalk and the trophoblast a great mass of coagulated material. This feature seems to be peculiarly characteristic of Procavia and as far as I can ascertain, has not been reported in any other animal. After this the embryonic disc flattens out and, as a result, the mesoderm is drawn out into a thin strand of cells. These cells ultimately form the splanchnic mesoderm in much the same way as the thinning out of the connecting stalk in Elephantulus (VAN DER HORST 1943) contributes towards the formation of the splanchnic layer of the exocoelomic cavity in that animal. It should be pointed out that in both Galeopithecus and Procavia the formation of the connecting stalk in no way assists in the development of the allantois as is the case in the higher Primates.

In the majority of animals, even of such widely divergent types as Manis, Sorex, and Lemurs, the mesoderm develops rather late and arises then from the primitive streak. Procavia, on the other hand, must be added to the list of those animals like Galeopithecus, Tatusia and Elephantulus as well as Tarsius, Cebus and other Primates which exhibit a precocious mesoderm-formation, and in which mesoderm is present long before the primitive streak has differentiated.

The origin of this precociously formed mesoderm seems to be rather difficult to determine. In Tarsius, Cebus and Hapale, the actual origin of the extra-embryonic mesoderm has not yet been definitely described. HILL (1932) suggested that in Tarsius "In all probability it is formed by proliferation from the caudo-median margin of the shield ectoderm, as HUBRECHT concluded." Likewise, in describing the extra-embryonic mesoderm of the Pithecoid types, Hapale and Cebus, HILL says "We have thus no knowledge of its first origin, but in early blastocysts of Hapale and Cebus there is evidence of the existence of a median area involving the hinder margin of the shield ectoderm and the immediately adjoining amniotic ectoderm which is in proliferative continuity with the extra-embryonal mesoderm." In the human blastocyst the "primary" mesoderm appears as a delicate, cellular reticulum which fills the cavity of the minute blastocyst. It has been described as being separated off in the morula

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stage (STIEVE 1926) and as being derived from the amnio-embryonal cell mass or the trophoblast (STREETER 1926).

On the other hand, HUBRECHT (1919) described the initial appearance of extra embryonic mesoderm in Galeopithecus as occurring in the neck of the embryonal cylinder where this cylinder is attached to the blastocyst wall. This is also the case in Procavia where the mesoderm appears first as a group of cells in the attachment stalk. HUBRECHT (1919) goes on to describe the mesoderm formation in Galeopithecus as follows: "An der Kaudalseite geht das sogenannte, ventrale Mesoderm aus dem Schwanzende des Ektodermcylinders hervor. An der Seite und vorn beteiligt sich das Ektoderm an der Bildung der annularen Mesodermzone." In Procavia it is also evident that proliferation of mesoderm takes place most rapidly at the caudal end probably from the ectodermal cylinder and that the mesoderm spreads out laterally in the amnio-embryonic vesicle between its ectoderm and entoderm. This lateral mesoderm is derived from stalk mesoderm. However, in addition, in the anterior region of the amnio-embryonic vesicle, the entoderm also participates in mesoderm formation as in Galeopithecus and also in Elephantulus (VAN DER HORST 1943). PATTERSON (1913) has described the proliferation of extra-embryonic mesoderm in Tatusia from the embryonic ectoderm of the amnio-embryonic vesicle just below its junction with the amniotic ectoderm. This is probably also the case in Procavia as shown in embryo VIII.

A striking feature of the development of the extra-embryonic membranes in Procavia is that the splanchnic mesoderm covering the free surface of the yolk-sac, and the mesoderm of the amnion develop earlier than the chorionic mesoderm. This splanchnic mesoderm has, therefore, spread out over a wider area of the yolk-sac than the chorionic mesoderm in the stages here described. However, neither splanchnic nor chorionic mesoderm has reached the ab-embryonic pole of the yolk-sac. Therefore, in this region the wall is only a bilaminar omphalopleure. In this respect Procavia differs from animals like Loris, in which the yolk-sac, at an early age, already has a complete wall of its own and a chorion which is vascularized all round.

PLACENTATION OF PROCAVIA CAPENSIS.
DESCRIPTION OF NON-PREGNANT UTERI.

The three non-pregnant uteri which have been examined may be classified as follows:—

I. Dioestrous uterus.
II. Early proestrous uterus.
III. Oestrogenic uterus.

They are dealt with in the above order and in each case a description is given of the uterine epithelium, stroma, and uterine glands.

I. DIOESTROUS UTERUS.

Uterine epithelium.

This is fairly uniform in width throughout and is not much convoluted. The epithelial cells are columnar in form but are very swollen. Their nuclei are oval in shape and scattered in distribution. They have apparently no distinct position in the cells but, if anything, tend to be situated nearer to the uterine lumen.

These cells, especially at the anterior end of the uterus, have a very ragged appearance due to their projection of peculiar, short cytoplasmic processes into the uterine lumen. In some parts these projections are so uniform in size and arrangement that they have the appearance of velvet (Pl. VI, Fig. 28). KEIBEL and MALL (1910) have made this statement when describing the human uterus: "In the premenstrual stage the mucous membrane rapidly thickens to two or three times its previous thickness. This depends partly upon the increase of oedema and partly upon the enlargement of the individual elements. This shows itself in the gland cells by a swelling of the nuclei and of the plasma and by abundant secretion which produces a frayed appearance on the inner surface of the cells; the secretion which is also found in the lumen of the uterus is now clearly recognisable histologically as a mucous secretion." As this frayed appearance of the free ends of the cells also occurs in the glandular epithelium of Procavia at this stage, it seems likely that in this animal it is also indicative of secretory activity, although little secretion was found in the lumina of glands or uterus.

One of the most striking characteristics of the uterine wall at this stage is the presence in it of an abundance of polymorph leucocytes. These are found in very great numbers in the sub-epithelial part of the stroma. They migrate through the uterine epithelium and may pass into the uterine lumen (Pl. VI, Fig. 28). There are, however, very few such leucocytes in the deeper layers of the stroma. Lying with these polymorph leucocytes, which have been liberated into the lumen, are also some degenerate red blood corpuscles, but no indications of bleeding in the stromal tissue could be located.

Stroma.

On the whole, this has a congested and dense appearance at the anterior end of the uterus but lower down the cells are becoming swollen and sodden.

At the anterior end of the uterus the stromal cells have a very uniform arrangement but the tissue lying immediately below the uterine epithelium

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shows definite signs of disintegration. The individual cells in this area are enlarged and swollen and have become separated from one another, giving this sub-epithelial zone a torn and ragged appearance.

The other cells of the stroma are spindle-shaped and all have small, oval, vesicular nuclei. In many of the cells distinct vacuoles are present. The stromal cells are all connected in such a way that they appear to form concentric rings of latticelike tissue round each gland and blood-vessel; so much so that, under the high power of the microscope, the tissue has a superficial resemblance to that of bone tissue, which in transverse section shows the Haversian canals surrounded by bone lamellae (Pl. VI, Fig. 29). It is interesting to note that ASSHETON (1906) made a similar comment when describing the trophospongia of the cotyledon in the uterus of a sheep on the 17th day of pregnancy. Of this he said: "The trophospongia of the cotyledon is more crowded with nuclei, which show a marked tendency to arrange themselves round the blood capillaries of the deeper portion; so that in section this part has the appearance of being made up of many systems of cells recalling the arrangement of cells in the Haversian systems of bone."

Lower down the uterus of Procavia this arrangement is obscured because parts of the stroma have become oedematous so that it has a homogeneous pink appearance when stained with HANSEN's haematoxylin and eosine. Round some of the glands, however, the latticelike concentric arrangement persists.

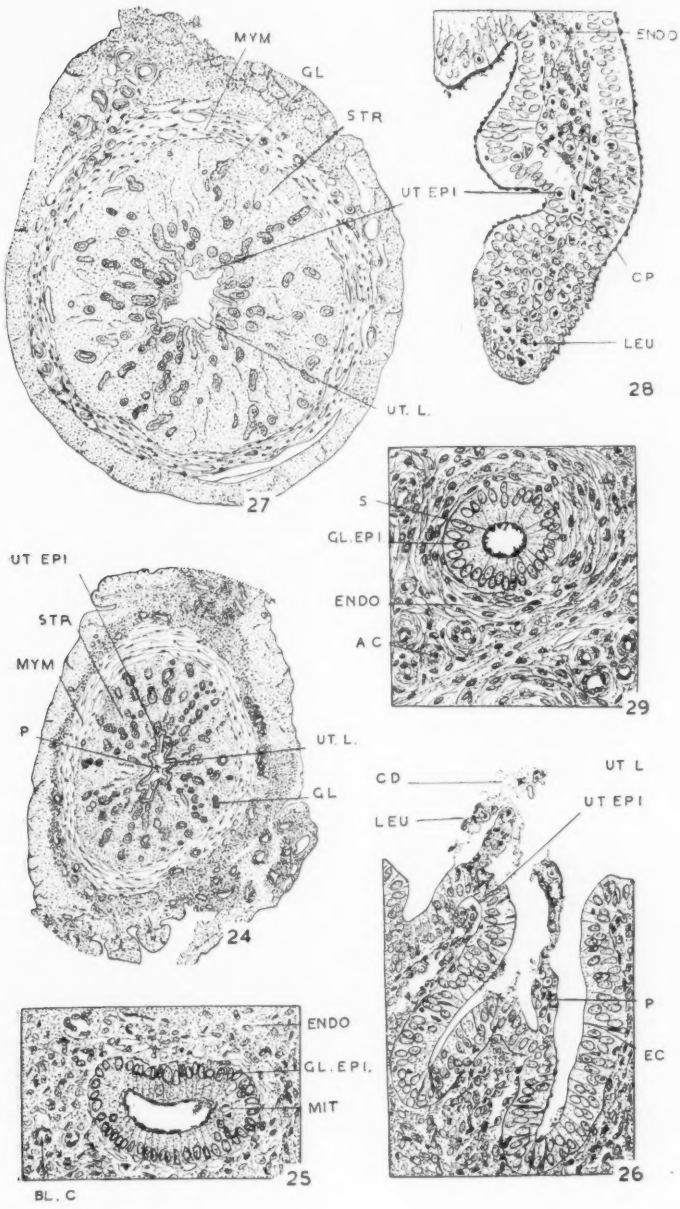
Blood capillaries are very numerous throughout the stroma but do not show dilation in any part of the uterus. Their arrangement is, however, noteworthy. Anteriorly they follow a tortuous course but mainly parallel with the long axis of the uterus so that in section they mostly appear to be cut in the transverse plane. More posteriorly, however, those occurring in the central part of the endometrium are cut obliquely or in longitudinal section and it is apparent that they are converging on the uterine lumen.

PLATE VI.

Fig. 24. A cross-section of the non-gravid, proestrous uterus to show the arrangement of the uterine tissues and glands. × 12.—Fig. 25. A section of a gland in the proestrous uterus showing the movement of the nuclei towards the lumen of the gland when mitosis is about to occur. × 180.—Fig. 26. Shows the emergence of a fingerlike papilla from the uterine epithelium of the early proestrous uterus. Note the healthy appearance of the cells below it, and the presence of elongated, narrow cells with tapering nuclei among the normal, columnar epithelial cells. × 180.—Fig. 27. A cross-section of the dioestrous uterus. Note the arrangement of the glands. Each has a bifurcated fundus, twisted body, and fairly straight neck. The lumina of the glands are small. × 12.—Fig. 28. Shows part of the thickened uterine epithelium of the dioestrous uterus. Note the scattered arrangement of its nuclei, the great numbers of polymorph leucocytes and the presence of regular cytoplasmic projections from the free surfaces of its cells. × 180.—Fig. 29. Shows part of the endometrium of the dioestrous uterus with the concentric arrangement of the connective tissue round the glands and blood-vessels. × 180.

THE EARLY EMBRYOLOGY OF PROCAVIA CAPENSIS

PLATE VI.



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Glands.

The glands are distributed over the whole circumference of the uterus but are less numerous in the more anterior region nearer the oviduct. In this anterior part, the glands are loosely looped so that in transverse section the cut parts of the glands are more or less evenly scattered throughout the stroma, being about the same distance apart and not arranged in distinct radiating rows as at proestrus. More posteriorly, however, the glands are most conspicuous and in this area they are more tightly coiled and open widely into the uterine lumen. Each gland consists of a fundus which is bifurcated, a twisted body and, in most cases, a straight neck which opens into the uterine lumen. The glands are not swollen and their lumina remain narrow (Pl. VI, Fig. 27). There is no appreciable difference in the width of the lumen of fundus, body and neck regions as is the case in the oestrogenic uterus. The nuclei in the cells of the glandular epithelium are mainly placed close to the basement membrance (Pl. VI, Fig. 29). Mitotics are found but are not numerous—never more than four per section.

II. EARLY PROESTROUS UTERUS.

Uterine epithelium.

This consists of large columnar cells which form a distinct layer of uniform thickness throughout the length of the uterus. The nuclei of these cells are relatively large, pale in colour and oval in shape. They are vesicular nuclei containing one to several nucleoli. Their position varies from the middle of the cell to the basal third.

Here and there fingerlike, or irregularly-shaped, papillae emerge from the epithelium (Pl. VI, Fig. 26) and project into the lumen. These obviously consist of degenerate cells, of polymorph leucocytes and other deeply staining bodies of irregular shape, which are probably pycnotic nuclei. Such outgrowths eventually become dislodged from the epithelium and fragments can be seen lying with glandular debris in the uterine lumen. Had this dislodgement of tissue occurred over a wider area of the uterine epithelium, it might have been compared with a process of menstruation except that in Procavia it is definitely not accompanied by bleeding. The cells of the epithelium in those regions where these outgrowths appear show no disorganisation, and their nuclei, which are placed below the point from which the papillae develop, remain healthy and clearly visible. In no instance was there any sign of the whole width of the epithelium being affected.

It seems pretty certain, therefore, that this uterus shows the conclusion of the process started in Specimen I, in which the leucocytes had already started to migrate through the uterine epithelium and the subepithelial tissue was

starting to disintegrate following the absence of fertilization. This is further substantiated by the fact that in this specimen the subepithelial tissue, except in a few small areas, consists of normal, healthy cells similar to the rest of the stroma, while polymorph leucocytes are completely lacking in this region. The papillae, therefore, represent the last vestiges of the changes brought about during the dioestrous phase described above, when fertilization failed to take place after ovulation.

Scattered at intervals between the cells of the epithelium are very elongated, narrow cells containing long, tapering, deeply-staining nuclei, (Pl. VI, Fig. 26), and resembling very closely those cells described by MARSHALL and JOLLY (1905). Such cells were observed in the Dog during the period of destruction of Proestrum. Since their appearance coincided with the increase in mucous secretion, a secretory function was assigned to them. Although they occur in Procavia during an earlier stage of proestrus, they are also probably secretory in function, especially as they occur in the glandular epithelium as well.

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Stroma.

This is compact and congested throughout the length of the uterus. The blood-vessels remain small and there is no indication of bleeding into the uterine cavity. Scattered throughout the stroma there are, however, aggregations of brown material which have probably been derived from previously extravasated blood. Similar brown material was observed by ASSSHETON (1906) in the six day's pregnant uterus of the sheep, and were described by him as being possibly "collections of dead, red blood corpuscles, the result of proestrous extravasation."

Glands.

Glands are conspicuous even in the most anterior region of the uterus and their ducts extend throughout the width of the stroma. These ducts are coiled but the course of the duct can easily be traced even in one section, because the cut parts of the glands are arranged to form, as it were, rows radiating from the lumen of the uterus towards the myometrium (Pl. VI, Fig. 24). In this respect the glands of Procavia can be compared with Elephantulus where VAN DER HORST and GILLMAN (1941) have noted that "Just prior to ovulation the glands are slightly coiled." In that part of the uterus which adjoins the oviduct, the lumen of the fundus part of each gland is noticeably wider than that of either the body or the neck of the gland as is the case in the oestrogenic uterus, but more posteriorly in the uterus the lumina of the glands do not show this variation in size at proestrus.

Elongated cells such as described in the uterine epithelium also occur among the cells of the glandular epithelium. These probably have a secretory function.

This increased secretory activity of the glands has been observed in the period of growth of proestrum in animals like the Ferret (MARSHALL 1904).

A few mitotics can be found in the glandular epithelium but only about three per section. It is obvious that in most instances where a cell is to undergo mitosis, the nucleus moves away from the basal wall of the cell nearer to the lumen of the gland (Pl. VI, Fig. 25).

III. OESTROGENIC UTERUS.

Uterine epithelium.

The most conspicuous change in the condition of the epithelium in this specimen when compared with the previously described uteri, lies in the position of the nuclei in the cells. In this oestrogenic uterus, the nuclei are definitely placed nearer to the lumen, in some places even touching the peripheral walls of the cells. The nuclei are, however, scattered, varying in their position from one cell to the next. Thus they cannot be said to be arranged in one or two rows as is the case in other animals like Elephantulus (VAN DER HORST and GILLMAN 1941) at this time.

At the anterior end of the uterus the epithelial cells have a rather ragged appearance due to their close association with the coagulum in the uterine lumen, but more posteriorly this does not occur and the uterine epithelium appears as a clearly defined row of tall, columnar cells.

A few leucocytes occur in the anterior region but these are completely lacking more posteriorly.

Stroma.

An intense oedema gives the uterus a sodden appearance, particularly between the glands (Pl. VII, Fig. 30) round which the concentric, latticelike

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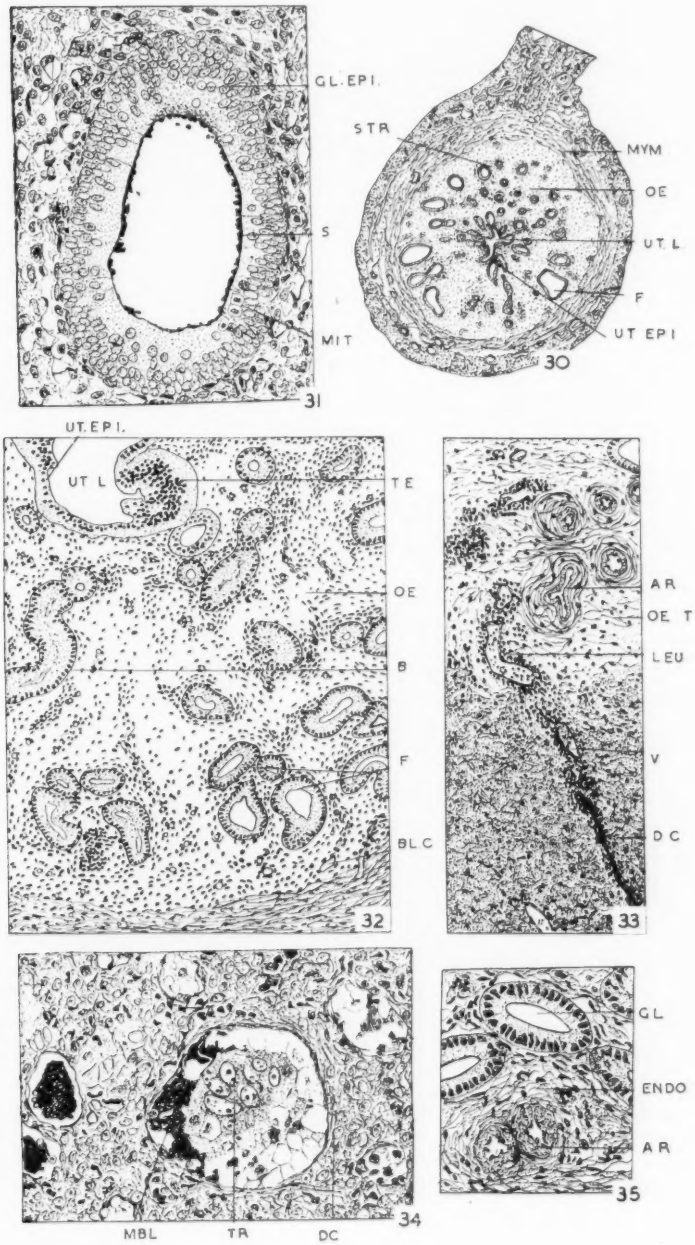
PLATE VII.

Fig. 30. A cross-section of the oestrogenic uterus to show the presence of interglandular oedema. Note the enlarged lumina of the glands and the characteristically dilated fundus region of each. × 12.—Fig. 31. A cross-section of a gland in the oestrogenic uterus. Note the secretion in the lumen, the presence of mitotics and the tendency of many of the nuclei in the cells of the glandular epithelium to move nearer to the uterine lumen. × 180.—Fig. 32. Shows part of the uterine wall of specimen I with its thickened uterine epithelium, nuclei clustered nearer to the uterine lumen and the concentration of oedema between its glands. Note the tightly-coiled fundus region of each gland. × 60.—Fig. 33. A composite diagram showing the bifurcation of an artery in the peripheral part of the endometrium of specimen III, and also a vein with aggregations of leucocytes all along its course and in its lumen. × 60.—Fig. 34. Shows the tip of a trophoblastic papilla which has invaded a maternal blood lacuna at the pole of the implantation area in specimen V. Note that the wall of the lacuna is as yet unaffected by the trophoblastic cells. × 180.—Fig. 35. Shows the structure of the glandular epithelium characteristic of the few remaining glands present in the peripheral part of the endometrium of specimen V. × 180.

THE EARLY EMBRYOLOGY OF PROCAVIA CAPENSIS

PLATE VII.



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arrangement of the cells described at dioestrus may still be observed only at the end of the uterus which adjoins the oviduct. More posteriorly the oedema seems to be evenly distributed. The intracellular fluid causes a uniform swelling of all the stromal cells and, therefore, the nuclei appear to be evenly distributed throughout the stroma. This provides a sharp contrast to that of the pregnant uterus in which the intensification of oedema occurs in patches between the glands. In these areas, although the fluid is still intracellular, the nuclei are pushed to one side of the cells and, therefore, appear more widely separated than elsewhere. Such zones have a homogeneous pale pink appearance as opposed to the condition elsewhere in the pregnant uterus, and throughout the oestrogenic uterus, where the cells of the stroma appear confluent and rather diffuse. In the subepithelial area the oestrogenic stroma is more dense, although even here the individual cells show enlargement.

Small blood capillaries are as numerous as in the dioestrous uterus, and many could be seen converging on the lumen. Blood-vessels in the myo- and mesometrium are large and well-developed.

Glands.

These are large and open widely into the uterine lumen. The lumen of each gland is noticeably wider than at any stage yet described. Each gland consists of a wide fundus region, seen in section as a large chamber lying below the myometrium, a coiled, narrow body and a fairly wide, straight neck which opens into the uterine lumen (Pl. VII, Fig. 30). In some of the glands the fundus is bifurcated as at dioestrus. As in the uterine epithelium, the nuclei of the glandular epithelium are definitely moving nearer to the lumen, although many are still basally placed. Mitotics are more common than in either the dioestrous or proestrous stages (Pl. VII, Fig. 31).

Indications of the secretory activity of the cells can be seen at their free edges but there is little coagulum in the lumina.

DESCRIPTION OF PREGNANT UTERI AND EARLY DEVELOPMENT OF THE PLACENTA.

In this section of the paper placental development is traced through those 10 specimens which are listed in the introduction and which have already been described in relation to embryonic development. In addition, two other pregnant uteri have been selected, a study of which helps to provide valuable information about the placentation of Procavia. These form the link between the present investigation and information supplied by earlier workers in this field. The two additional specimens are:

Embryo XI—27-somites stage.

Uterine swelling 12 mms. in diameter.

Embryo XII—48-somites stage.

Uterine swelling 14.5 mms. in diameter.

SPECIMEN I.

Uterine epithelium.

The uterine epithelium is no longer of uniform width throughout but in many places has become considerably thickened (Pl. I, Fig. 1 and Pl. VII, Fig. 32): Indicative of this proliferative activity of the epithelial cells are the numerous mitotic figures found in such swollen areas, where the nuclei are particularly concentrated. In these parts the form of individiual cells is obscured. The width of the epithelium may be quite twice as great at that of the normal, columnar cells found in those parts of the uterine epithelium which have not yet undergone thickening.

The vesicular nuclei are oval in shape, have two nucleoli and contain numbers of darkly staining chromatin granules scattered throughout the karyosome. Particularly in the thickened parts of the epithelium, the nuclei are placed in the two-thirds of the cells lying nearest to the uterine lumen. The deeper one-third of the cells is, therefore, left completely free and this zone between the clearly defined basement membrane and the densely nucleated zone is occupied only by clear cytoplasm of a homogeneous pink appearance after staining (Pl. I, Fig. 1 and Pl. VII, Fig. 32).

Stroma.

The stroma is made up of attenuated cells forming a loose, latticelike tissue which is oedematous but rather different in appearance from that of the oestrogenic uterus. Whereas the latter has a diffuse, sodden appearance over its whole area, the oedema in this pregnant uterus is concentrated more especially between the glands and blood-vessels, so that the nuclei appear to be aggregated round the glands, being pushed out of position by the oedema. The nuclei of the stromal cells are elongate and oval in shape.

The loose, latticelike arrangement of the cells occurs in some parts even of the subepithelial zone but in other places the cells in this region show the diffuse, sodden appearance characteristic of the oestrogenic uterus.

The blood supply is still confined to a fine network of tiny capillaries scattered throughout the stroma. No large vessels are present and the straight capillaries, which were found converging on the uterine cavity, especially in the oestrogenic and dioestrous uteri, could not be identified here.

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Glands.

Glands are plentiful throughout the length of the uterus. They seem to reach their maximum development at this time, for in the uteri containing older embryos the number and size of the glands becomes progressively reduced. The morula and earlier embryos lie completely free in the uterine lumen. Glandular secretion, which constitutes the embryotrophe in the uteri containing these early stages, must, therefore, be responsible for the nourishment of them, until they become attached to the uterine wall.

The structure of the glands in this uterus is very different from that of the glands occurring in the dioestrous, proestrous and oestrogenic uteri. The fundus region of the gland is no longer bifurcated as at dioestrous, nor is it in the form of a wide chamber as at oestrus. Instead it consists of a narrow tube which is tightly coiled into a ball (Pl. VII, Fig. 32). The body and neck of each gland lead imperceptibly into one another forming an almost cork-screw-like tube instead of the loose, irregular loops as at oestrus, or the smaller, regular coils characteristic of the proestrous uterine glands. The lumina of the glands are not quite as wide as those in the oestrogenic uterus, nor do the necks of the glands form wide, straight tubes before opening into the uterine lumen, as they do at oestrus.

The glandular epithelium remains thick but the nuclei are basally placed and form a single row. Hardly any mitotics were found.

SPECIMEN II.

A. Maternal tissues.

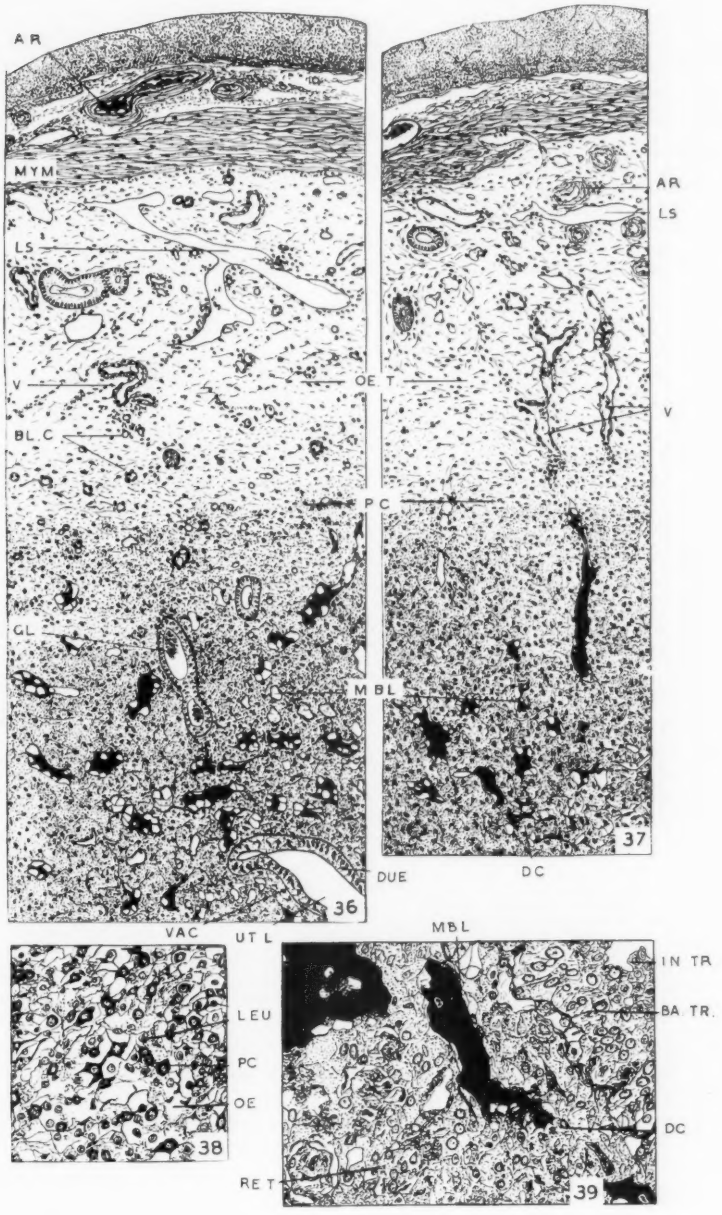
Uterine epithelium.

At the place of implantation the uterine epithelium has for the greater part already been destroyed (Pl. I, Fig. 4). Even outside the area of attachment of the blastocyst, where the uterine epithelium is still intact, it is clear that it has been affected by the pregnancy.

PLATE VIII.

Fig. 36. A cross-section of part of the uterine wall of specimen II in the non-implantation zone. Note the degenerating uterine epithelium, the cut blood-vessels and capillaries, lymph spaces and gland containing blood extravasates and secretions. The endometrium is clearly divided into an outer oedematous zone and an inner decidua compacta containing dilated capillaries. × 60.—Fig. 37. Shows a similar area of uterus II to that given in Fig. 36. Note the vein leaving the myometrium, a vein branching in the outer part of the endometrium and the straight part of a vessel passing through the decidua compacta. × 60.—Fig. 38. Shows the formation of predecidual cells and the leucocytes present in the area between the outer oedematous tissue and the inner decidua compacta of specimen III. × 240.—Fig. 39. Shows the reticulum present at the border of the invading trophoblast in specimen III. Note the rounded mass of tissue on the left side of the diagram which is clearly demarcated from the rest of the decidua compacta. × 240.

PLATE VIII.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In parts immediately adjacent to the implantation site, the cells of the uterine epithelium show definite degeneration (Pl. VIII, Fig. 36). Their cell walls are wavy in outline, vacuoles are plentiful, and their nuclei have become pycnotic. The latter show irregular shapes and their nucleoli and chromatin granules are no longer visible, due to their dark staining reaction. Even further away from the attachment area, the epithelial cells show some changes. Thus in those parts of the uterus some distance in front and behind the point, where the blastocyst is attached, the uterine epithelium shows the presence of vacuoles. The nuclei of its cells are becoming irregular in outline, but all show the normal, pale staining reaction. In most of these cells the nuclei are centrally placed, if anything slightly nearer to the uterine lumen than to the clearly defined basement membrane.

It seems reasonable to suppose, therefore, that these changes, in regions neighbouring on the implantation zone, represent progressive stages in the degeneration of the uterine epithelium, which culminate in the destruction of this tissue, as the trophoblast spreads out over a wider and wider area.

Stroma.

Two distinct zones are discernible in the stroma as shown in Pl. IX, Fig. 40.

I. An outer, loose, spongy region immediately below the myometrium in which many of the cells have vacuoles and are oedematous, so forming a latticelike tissue. In this region are large lymph spaces (Pl. VIII, Fig. 36), a network of fine blood capillaries and the coiled fundus parts of the few, remaining uterine glands (Pl. VIII, Figs. 36 and 37).

II. A dense, compact inner zone which becomes relatively more extensive at the site of implantation. In this region leucocytes are plentiful.

At the outermost fringes of the compact zone, i.e. where the oedematous cells merge into the more dense tissue, predecidual cells can be identified which are similar to those described by VAN DER HORST and GILLMAN (1941) in Elephantulus. The smallest of these cells at the outermost edges of the compact region are regular in outline consisting mainly of a pale, central nucleus surrounded by a homogeneous, round mass of cytoplasm, which is non-granular and has a fairly deep pink staining reaction. As these cells enlarge in size and become more numerous in regions nearer to the uterine lumen, they lose their regular outline and become angular in form. Similar cells are described in the stroma of specimen III and pictured in Pl. VIII, Fig. 38.

Still closer to the uterine lumen these cells completely replace the oedematous cells and are so closely packed together that their tapering processes dovetail into one another. In this way a dense reticulum composed of large decidual cells and connective tissue fibres is formed between the dilated capillaries,

which are a characteristic feature of the subepithelial area. A similar arrangement occurs in specimen III (Pl. VIII, Fig. 39).

Glands.

By comparison with the condition in the non-pregnant uteri and in that containing the morula, the glands in this specimen are few in number and poorly developed. The description given by THURSBY-PELHAM (1924) for the glands of a specimen with a uterine-swelling of 8 mms. diameter, might easily be applied here. She said that the uterus in transverse section showed "a layer of somewhat loose tissue in which are the remains of the glands ... They have diminished greatly in size and are found scattered here and there all round the uterus; their lumina are small and they are evidently taking no further part in the nourishment of the embryo." Below the myometrium, cut parts of the coiled fundus regions of the glands give the appearance, in any one section, that glands are confined to this area. However, here and there a straight duct could be traced through the compact part of the stroma. These ducts converge on the uterine lumen. In the lumina of such ducts blood extravasates and leucocytes are often present as in Pl. VIII, Fig. 36. The glandular epithelium is almost cuboidal in form and its chromatic nuclei are basally placed and of a narrow, oblong shape. No mitotic figures were found in this tissue.

Blood-vessels.

The most striking change which has occurred in the uterus of specimen II when compared with the condition already described in the uterus containing the morula is the intense vascularization of the stroma.

Blood-vessels leave the main arteries and veins in the myometrium and enter the endometrium at various points. These vessels, especially the arteries, are associated with a branched network of fine capillaries. In addition, each artery follows a very tortuous course. It is, therefore, difficult to trace them accurately. Some interesting observations have, however, been made.

The course of each artery seems to be as follows: After emerging from the myometrium it becomes coiled, but follows this twisted course only through the outermost one-third of the endometrium, where the tissue is mainly of an oedematous nature. In this region also the arteries give rise to a system of fine, branched capillaries which form a tangled network and are definitely linked up with similar venous capillaries. Such capillaries are conspicuous at this stage of development but are also characteristic of specimen V. Many are shown cut in transverse section in Pl. VIII, Fig. 36, and in Pl. IX, Fig. 41 a few can be seen branching off the main arterial trunks. Following these main arterial trunks through the stroma towards the uterine lumen, it was found that in the middle third of the endometrium, where the predecidual cells are

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being formed, they straighten out and pass radially inwards. Thus in many sections distinct elongate channels could be seen cut longitudinally and extending from the oedematous zone to the subepithelial region. Such straight vessels are much more numerous at the implantation site than elsewhere. Whereas sections cut above or below this area show two or three straight channels, those cut through the place of attachment of the embryo show anything from seven to thirteen per section. In no instance were these straight vessels found to branch in this part of the stroma.

On reaching the innermost third of the endometrium where the dense reticulum is fully developed, the straight channels enlarge and lead into a system of lacunae, all of which are dilated, have thin walls and are filled with blood. This lacunar system lies just below the uterine epithelium in the subepithelial area (Pl. VIII, Figs. 36 and 37). In this specimen it is not possible to trace the main vessels beyond their point of entry into this subepithelial, lacunar system. Consequently, it is difficult to say whether the arteries become coiled again or whether they branch to form capillaries which produce the dilated lacunae.

The structure of the walls of the arteries is also worthy of special comment. In the myometrium and at the periphery of the endometrium, just below the uterine muscles, the walls of the arteries are clearly provided with all three layers, including a distinct muscularis (Pl. VIII, Figs. 36 and 37). However, as these arteries give rise to branched capillaries and begin to straighten out on entering the middle region of the endometrium, this muscular layer of their walls becomes more and more reduced. Finally, in those parts of the straight channels passing through the compact decidual tissue, the arterial walls have completely lost their muscular coat and are composed only of a thin layer of endothelium. This phenomenon becomes even more pronounced as pregnancy advances. Pl. XI, Fig. 48 shows a portion of an artery in specimen V in which the muscular coat has been lost in the part of it which lies nearest to the uterine lumen i.e. on the left side of the diagram. The loss of this thick wall in the arteries makes it practically impossible to differentiate arterial from venous channels near the uterine lumen and it is really only by following the straight channels through their coiled parts to their origin in the myometrium

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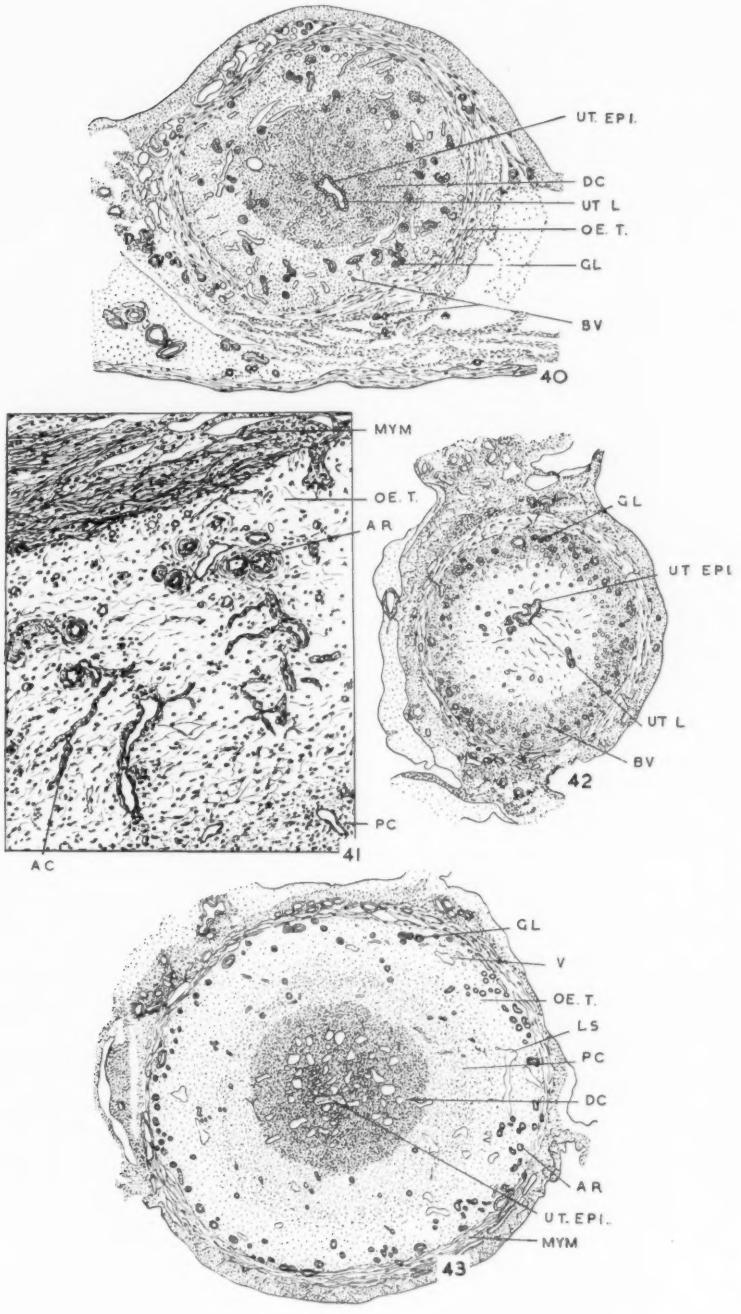
PLATE IX.

Fig. 40. A cross-section of the whole uterus of specimen II to show the distribution of tissues, glands, blood-vessels and lymph spaces. × 12.—Fig. 41. A composite diagram to show the capillaries branching from the main arterial trunks in the oedematous, outer zone of the endometrium of specimen II. × 60.—Fig. 42. A cross-section of the uterus of specimen V in the non-implantation area. Note the presence of oedema in the inner half of the endometrium only. × 12.—Fig. 43. A cross-section of the same uterus as is shown in Fig. 42, showing the distribution of oedema, predecidual cells and decidua compacta nearer to the implantation site. × 12.

PLATE IX.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that the differentiation can be made. In the lacunar system it is likewise impossible to distinguish an arterial from a venous lacuna.

The veins follow a very similar course to the arteries except that in the oedematous zone some of them appear to branch as well as giving rise to small capillaries (Pl. VIII, Fig. 37). On leaving the maternal lacunar system the veins pass through the stroma as straight channels and are often dilated. Entering the outer zone of the endometrium, however, they become twisted and receive capillaries. Finally these veins open into the main venous channels lying in the myometrium. On the whole the diameter of the venous channels in the stroma which leave the maternal lacunar system is greater than that of the straight arterial vessels.

B. Foetal tissues.

The arrangement and structure of the foetal tissues, as well as the destruction of the uterine epithelium and the attachment of the trophoblast which initiates the development of the placenta have been described in detail earlier in this paper, in the section dealing with the embryology of specimen II.

SPECIMEN III.

A. Maternal tissues.

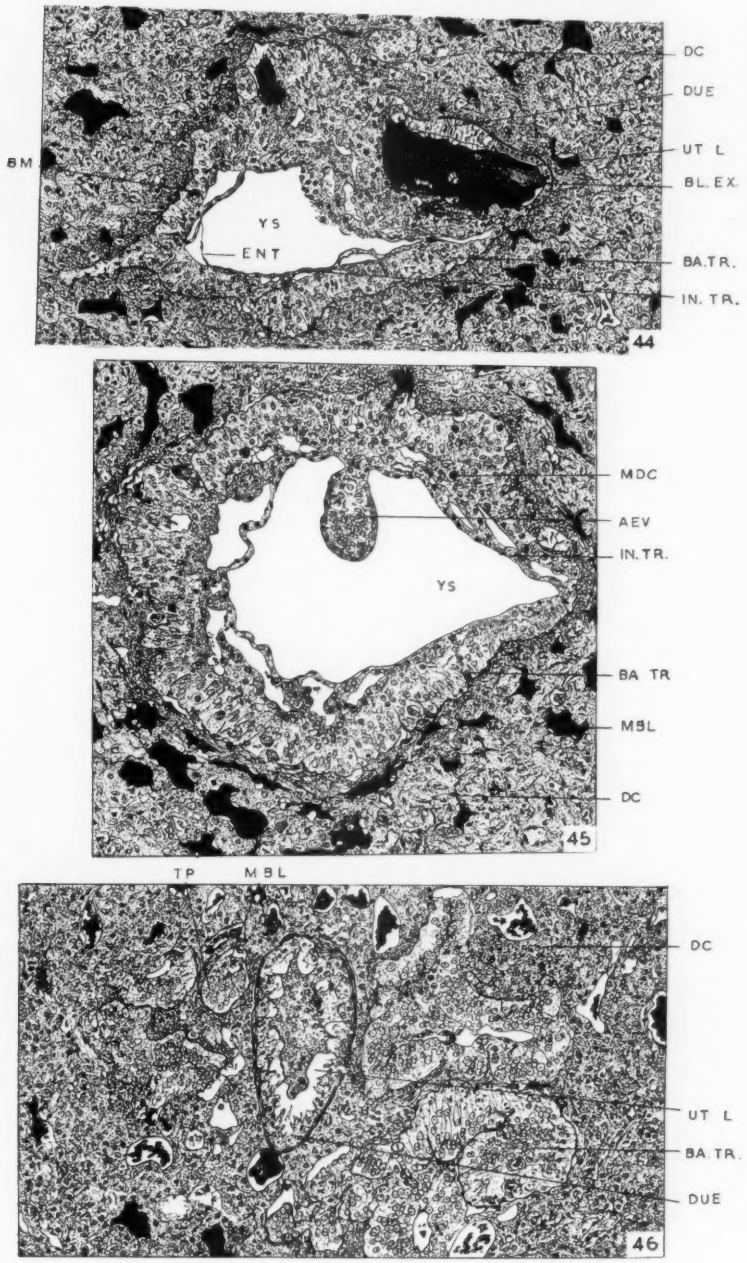
Uterine epithelium.

As in specimen II, the uterine epithelium of specimen III shows difference in structure related to its proximity to the implantation zone. Some distance in front and behind the embryo the uterine epithelium consists of normal, healthy, columnar cells and in places it shows thickenings as in specimen I containing the morula. Nearer to the attachment site the cells are more uniformly cuboidal in form and the same degenerative changes as were described in specimen II can be traced here. Finally at the place of implantation the uterine epithelium has been for the greater part destroyed. (Pl. X, Fig. 44.)

PLATE X.

Fig. 44. A cross-section through the implantation site of specimen III at the anterior pole, to show the destruction of the uterine epithelium and the method of attachment and penetration of the trophoblast. Note the proliferation of the trophoblast to form a lobed process on the upper side of the diagram, and the blood extravasates in the uterine lumen. × 90.—Fig. 45. A cross-section through the implantation zone of specimen III where the amnio-embryonic vesicle is attached. The basal trophoblast shows as a distinct cellular layer lying next to the maternal tissues, while the lacunar, inner trophoblast is also being differentiated. Note the maternal decidual cells lying in the basal trophoblast. Maternal blood lacunae occur all round the foetal-maternal border. × 90.—Fig. 46. A cross-section through the polar region of the attached blastocyst of specimen V. Note the initial penetration by irregular trophoblastic papillae into the uterine lumen and into the maternal blood lacunae. The uterine epithelium is degenerating all round. × 90.

PLATE X.



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At the two free poles of the embryo which lie in contact with the uterine lumen, this cavity is filled with blood extravasates. This is a feature which seems to be characteristic also of older stages of pregnancy.

Stroma.

Like the uterine epithelium, this part of the uterus also shows variations in the structure and distribution of its tissues depending on their proximity to the embryo.

In the non-implantation areas, the stroma consists mainly of fairly dense tissue throughout. Some of its cells are, however, filled with fluid and in others very large, clear vacuoles make their appearance. In this uterus, however, such cells do not occur in any particular region of the endometrium as is the case in specimens IV and V. Instead, groups of cells seem to be affected in this way. Such cells may be located anywhere in the endometrium from the sub-epithelial zone to the myometrium. Aggregations of brown pigment are numerous in the peripheral part of the stroma adjacent to the muscles.

The condition of the stroma at the implantation site is somewhat different. Differentation into an outer oedematous zone, an area in which predecidual cells are being formed, an inner compact zone (which may be termed the decidua compacta) can still be made as in specimen II. However, the relative extent of each of these areas is no longer the same. Instead of each region occupying about one-third of the width of the endometrium, the relative distribution is now:

Outer one-fifth of oedematous tissue,

Middle two-fifths showing predecidual cell-formation,

Inner two-fifths decidua compacta.

The outer oedematous zone consists of cells, most of which contain vacuoles which are even more pronounced and more regular in size than in the same area of uterus II. Their nuclei are spindle-shaped and darkly staining. This part of the stroma has a latticelike appearance and, as a result, the aggregations of brown pigment present, which are similar to those described in the early proestrous uterus, show up clearly against the pale background.

The encroachment of the trophoblast on the uterine tissues has obviously affected a greater area of the stroma than in specimen II, for predecidual cell formation is in progress over a relatively wider area of the uterus. These predecidual cells have distinctly rounded nuclei (Pl. VIII, Fig. 38) and the same structure as those described in specimen II. Present in this part of the stroma particularly are hundreds of polymorph leucocytes, which are even more abundant than in the stroma of the previously described uterus. The presence of all these leucocytes tends to give this zone a more congested appearance than in specimen II.

The inner two-fifths of the endometrium again consists of dense tissue. The cells of this decidua compacta have lost their regular shape and appear as confluent, decidual masses interspersed with connective tissue fibres. In several places, especially near the invading trophoblast, rounded masses of such tissue are clearly demarcated from the surrounding area (Pl. VIII, Fig. 39). Some leucocytes also occur in this part of the stroma.

Glands.

Glands are numerous in the non-implantation zones where each consists of a fairly wide fundus and a much coiled body which is looped loosely through the stroma and opens into the uterine lumen. At the implantation site, however, the number and structure of these glands is very similar to those in the uterus of specimen II already described.

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Blood-vessels.

When compared with the arrangement of the blood-vessels in specimen II certain changes are noticeable in this uterus, but on the whole the distribution and course of the arteries and veins is very similar. The main differences which were observed are as follows:

1. Arteries appear to be relatively more numerous than in the previous specimen. This is probably due to the fact that here the arteries may be bifurcate. In some instances this bifurcation occurs immediately after the artery enters the endometrium from the myometrium. In other cases the forking occurs after the artery has penetrated well into the oedematous tissue (Pl. VII, Fig. 33), but before it straightens out to form the unbranched, radial channel which passes through the predecidual tissue towards the decidua compacta.
2. The course of an artery is easier to follow mainly because it is more tightly coiled at the periphery than in specimen II. In addition, the capillary network which is such a conspicuous feature of specimen II is not developed to nearly the same extent here. In fact, very few capillaries could be found leaving the main arterial trunks.
3. The veins are less coiled at the periphery than the arteries. An outstanding feature of this uterus is that the course of the veins, especially through the oedematous zone of the uterus, is clearly demarcated by the aggregation of numbers of polymorph leucocytes in the tissue adjacent to the veins and in their lumina (Pl. VII, Fig. 33). This was not noticeable in specimen II.
4. As in the previous uterus, the straight venous and arterial channels lead from and into a well-developed, maternal lacunar system, lying in the decidua compacta. This specimen, however, shows quite clearly that these lacunae are formed by the dilation of branches of the main channels, a fact which

could not be definitely ascertained from a study of the same region in the uterus of specimen II.

It is of special importance to note that this lacunar system is as equally well-developed at the two poles of the blastocyst as in the equatorial plane, for in uteri containing older embryos this arrangement is changed.

B. Foetal tissues.

At the anterior and posterior ends of the embryo, the method by which the basal trophoblast invades the uterine tissue and destroys the epithelium can be followed. In Pl. X, Fig. 44, the foetal tissues are shown at the anterior pole of the developing placenta. In some places the uterine epithelium is still intact though undergoing degeneration, while in others the basal trophoblast has already destroyed and replaced the uterine epithelium, although the basement membrane is still intact. However, on the upper side of this diagram it can be seen that the proliferation of the trophoblast is taking place and a lobed structure composed of foetal cells is encroaching further into the stroma. This is probably making use of the blood extravasates in the uterine lumen for the nourishment of its cells. Penetration of the uterine wall is, however, at this stage of pregnancy, not in the form of fingerlike, trophoblastic processes, as it is in specimens IV and V. Instead, penetration of the uterine tissues takes place over the poles of the blastocyst by a more or less regular sheet of cells. This layer may be here and there enlarged by proliferation of its trophoblastic cells to form a lobe which penetrates the stroma to a greater depth.

In Pl. X, Fig. 45 the primordial placenta is seen completely surrounding the embryo. From this diagram it is clear that the trophoblast is composed of cellular tissue and must, therefore, be regarded as cytotrophoblast. Nowhere is there any indication of the presence of plasmoditrophoblast. Even at this early stage, however, the trophoblast can be clearly differentiated into two distinct regions. In describing these zones in the placenta of a specimen with a uterine swelling of 8 mms. diameter, THURSBY-PELHAM (1924) used the terms basal trophoblast and inner trophoblast. The basal trophoblast represented the "outer invading layer," and the inner trophoblast was "the lacunalised portion," nearest to the embryo. The same terms will, therefore, be used in this paper.

The basal trophoblast consists of a regular row of deep columnar cells. Each cell has a distinct, large, rounded or slightly oval nucleus. The contents of the nuclei have a pale staining reaction and, as a result, the one or two large nucleoli show up very clearly in each nucleus. This basal trophoblast is definitely phagocytic and in many places large maternal, decidual cells, which have been engulfed by it, can be seen lying within its boundaries. (Pl. X, Fig. 45.) Except at the two ends of the embryo, however, the depth of pene-

tration of this basal trophoblast is fairly even. In fact, the regularity of its cells might easily mislead one into regarding it as uterine epithelium unless the destruction of this layer had been previously witnessed.

In some places this basal trophoblast has already reached and destroyed the walls of the maternal blood lacunae (Pl. X, Fig. 45) and maternal blood is, therefore, flowing into the trophoblastic lacunae, which are being formed by the inner trophoblast on the foetal side of the basal trophoblast. However, as can be seen from Pl. X, Figs. 44 and 45, in this specimen the inner trophoblast is not yet a very extensive zone. It also consists of cellular tissue, but the cells of which it is composed are smaller than those in the basal trophoblast, and are polyhedral in shape. They contain small, round nuclei which stain darkly. These cells form trabeculae so that a wide-meshed foetal lacunar system or labyrinth is being built up on the foetal side of the primordial placenta but, as yet, this consists only of a single row of irregularly shaped lacunae. It is of special interest to note that these lacunae are completely surrounded by the polyhedral cells of the inner trophoblast and in no instance, therefore, do they come into direct contact with the basal trophoblast.

Closely applied to the foetal surface of the inner trophoblast is a single layer of cells, the entoderm of the yolk sac.

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SPECIMENS IV AND V.

Although showing uterine swellings which measured 7.2 mms. and 6 mms. in diameter respectively, specimens IV and V have a very similar placental structure. The sections which were cut of specimen V are, however, better for histological study, and the following description refers particularly to that specimen.

A. Maternal tissues.

Uterine epithelium.

Degenerative changes similar to those described in specimens II and III take place in the uterine epithelium of this specimen. Thus as the placental site is approached a transition can be traced from an epithelium consisting of healthy, narrow, columnar cells with small, oval, centrally placed nuclei to one consisting of cells which have become more cuboidal and in which the nuclei seem to have no definite position in the cells. Finally in those parts of the uterus where the decidua compacta is becoming vascularised the walls of the epithelial cells nearest to the uterine lumen break down completely. In this uterus, therefore, the degenerating epithelium has an even more ragged appearance than in the previous specimens. Vacuoles appear and many of the nuclei have been dragged from the cells and show as irregularly shaped, dark

bodies lying with the torn tissue. In Pl. X, Fig. 46 the first contact between the proliferating trophoblast and this ragged uterine epithelium can be seen. As in specimens II and III, the entire uterine epithelium and basement membrane have been destroyed where the trophoblast has become attached.

Stroma.

As in specimen III, this uterus shows considerable variation in its structure in relation to its association with the attached blastocyst. In this uterus of specimen V, however, the differentiation has perhaps become even more marked, as a comparison of Pl. IX, Figs. 42 and 43 will show.

In the non-implantation zones stromal oedema is definitely confined to the subepithelial region while the tissue lying just below the myometrium is of a compact nature. It should be noted that this congested appearance is not associated with a decidual reaction but it is due simply to the abundance of connective tissue cells in this area (especially between the glands) and to their large, darkly staining, elongated nuclei. These two zones, the oedematous and the compact, are about the same in extent in parts of the uterus some distance from the implanted blastocyst as can be seen in Pl. IX, Fig. 42.

In and around the implantation zone a marked change occurs in the distribution of the stromal tissues. By degrees the outer dense connective tissue cells become vacuolated and are sodden with fluid, thus increasing the oedematous area. Finally in that part of the uterus where the embryo is located, the uterus is much swollen, due partly to the complete replacement of the outer dense area by stromal oedema.

Meanwhile, however, changes have also occurred in the subepithelial area. Here, as the attachment area is approached, the oedema is gradually replaced by decidual cells, which form the decidua compacta below the uterine epithelium. The gradual formation of these cells in the form of predecidual cells can be observed at the fringes of this dense zone as was described in specimens II and III. The distribution of the oedematous cells, predecidual cells and decidua

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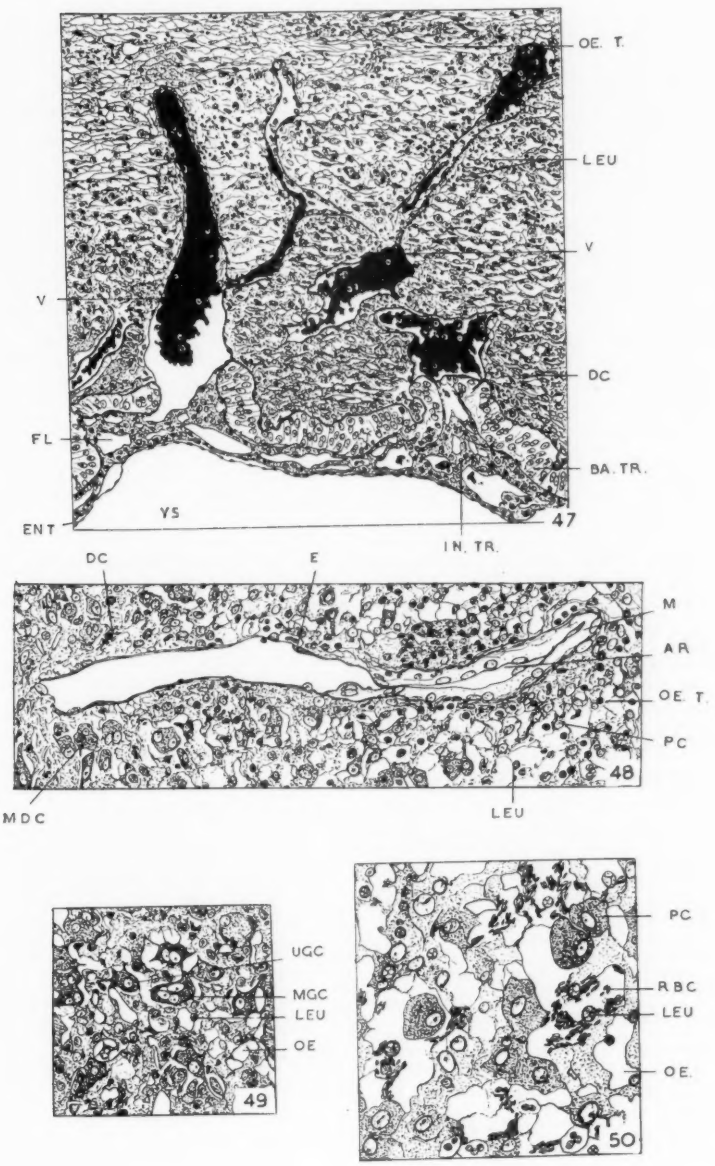
PLATE XI.

Fig. 47. Shows part of the endometrium and attached blastocyst of specimen V. The dilated extremities of two veins are shown which are interconnected by smaller branches. The vessel on the left has already been opened by the basal trophoblast. × 90.—Fig. 48. Shows the straight part of an artery lying in the endometrium of specimen V. The invading trophoblast would be located on the left side of the diagram. Note the loss of the muscular layer in the part of the arterial wall lying nearest to this side. × 240.—Fig. 49. Shows the first step in the formation of decidual giant cells from predecidual cells in the endometrium of specimen V. × 240.—Fig. 50. Shows the structure of the endometrial tissue on the myometrial side of the decidua compacta of specimen VI. Note the large nuclei of the oedematous cells, the predecidual cells, extravasated red blood corpuscles and polymorph leucocytes. × 420.

PLATE XI.



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compacta of stroma in the neighbourhood of the placenta is very similar to that of specimen III as can be seen in Pl. IX, Fig. 43.

One outstanding feature of the decidua compacta of this specimen is the first appearance of multinucleate decidual cells. In the previous specimens the decidual cells appeared mainly as a confluent reticulum except that, in specimen III, in some places just near the basal trophoblast, rounded masses of tissue had become demarcated off from the surrounding confluent cells. (Pl. VIII, Fig. 39.) The giant cells which appear in the decidua compacta of specimen V are clearly visible as irregularly shaped masses of clear cytoplasm containing two to several large vesicular nuclei as shown in Pl. XI, Fig. 49. Most of them appear to be binucleate but several were observed containing three or four nuclei. Such giant cells are most easily located at the edge of the decidua compacta, i.e. between the zone where predecidual cell formation is in progress and the decidua compacta proper. They are, moreover, mainly found at the two poles of the placenta, where the fingerlike protrusions of the trophoblast are penetrating the mucosa. Nearer to the uterine lumen, the giant cells, although present, cannot be discerned so easily owing to the dense, confluent nature of the decidua compacta.

Leucocytes are still particularly numerous in the oedematous and predecidual tissues. The brown aggregations of material seen in the outer part of the stroma of specimen III are not present here.

Glands.

The condition and distribution of the glands in this uterus is similar to that in specimen III. The glandular epithelium is obviously no longer active. As shown in Pl. VII, Fig. 35, it consists of cuboidal cells in which the nuclei have rather irregular shapes, are basally placed and stain very darkly.

Blood-vessels.

This specimen provides valuable information in regard to the development of the blood supply to the placenta. At the two poles of the blastocyst the arrangement of the blood-vessels and their connection with the placenta is different from that in the middle region. This condition did not occur in the younger specimens.

In front and behind the placental area, where the decidua compacta is gradually replacing the subepithelial oedema, the blood supply becomes more and more extensive as the implantation site is approached. Finally, at the two poles of the placenta the stroma surrounding the uterine epithelium appears as a wide meshed net in which the swollen capillaries are separated from one another and from the uterine epithelium itself only by thin strands of decidual cells. This is a lacunar system similar to that described in specimen III.

Connecting these lacunae with the coiled vessels below the myometrium are also straight, longitudinal channels. Thus in these parts of the uterine wall, viz. at the two poles of the placenta, a condition of vascularization exists similar to that already described as occurring all round the placental site of the embryo contained in the uterus which showed a swelling 5 mms. in diameter. The dilation of the blood capillaries round the lumen has also been observed in the uteri of other animals. For instance, similar phenomena have been reported in the macaque by WISLOCKI and STREETER (1938), who said: "Moreover the stroma in the neighbourhood of the ovum shows marked edema and the enlargement of the capillaries." In the macaque, however, these phenomena are definitely more localized than in Procavia on account of the difference in the form of the placenta.

The condition and arrangement of the blood-vessels in parts of the uterus adjacent to the equatorial plane of the placenta are rather different to that already described at the two poles. This applies particularly to the veins which are certainly the most conspicuous structures found in this part of the uterus. Below the myometrium these are somewhat twisted as in previous specimens. The wide, straight channels, which are continuous with the coiled parts, can also be located, but in this uterus these wide channels may be branched as well as giving rise to a conspicuous capillary network. All such venous channels are greatly dilated on leaving the trophoblast. In this area of the uterus, however, the irregular, netlike lacunar system which is so characteristic of the two poles of the placenta is not found. Instead, the greatly enlarged extremities of the veins may be interconnected just below the basal trophoblast by narrower branch vessels. This is clearly illustrated in Pl. XI, Fig. 47, which shows the swollen extremities of two such large veins linked by a common branch. The walls of some of these dilated vessels have already been destroyed by the basal trophoblast, but the endothelium of many of them on the other hand, although lying right against this phagocytic layer, is still intact. Both conditions can be seen in Pl. XI, Fig. 47 where one vessel (on the left-hand side) has been opened and the other (on the right-hand side) has not.

The arteries do not appear to be so numerous as the veins because they do not branch or become swollen to the same extent. They follow the same course as those described in specimen III, but in this uterus are associated with a more distinct capillary system as in specimen II. The straight arterial channels are still unbranched and even at their innermost extremity do not dilate or form a branched lacunar system, nor are they interconnected with other arteries as are the veins with neighbouring veins. Very few of them seemed to be penetrated by the trophoblast. As in earlier stages of pregnancy, however, the loss of the muscle layer from the wall of the arteries is an interesting feature. This can be clearly seen in Pl. XI, Fig. 48, which shows a part of a straight arterial channel cut longitudinally.

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Leucocytes remain a conspicuous feature. In this uterus they are present in small numbers in and around the arteries, but as in specimen III they occur more especially in association with the veins.

B. Foetal tissues.

The actual structure of the foetal placenta in this specimen is very similar to that already described in specimen III. It consists of basal and inner trophoblast. The only real difference lies in the fact that the extent of the inner trophoblast is slightly greater in this primordial placenta, so that the foetal lacunae are more numerous than in specimen III. The placenta is still circumferential and completely surrounds the embryo. However, just as the blood supply associated with the two poles and the equatorial zone of the placenta differed, so are there differences in the condition of the basal trophoblast in these regions which were not observed in the previously described placenta. The results obtained from a study of the extremities of the placental area are noteworthy because they give a clear picture of the method by which the trophoblast makes its initial penetration into the enlarged, maternal capillaries of the maternal lacunar system immediately surrounding the uterine lumen. Thus, at the two poles of the placenta, the proliferation of the basal trophoblast is obviously an irregular one and is in the form of fingerlike protrusions or papillae, whereas in the equatorial plane this basal trophoblast appears as an uniform though somewhat undulating layer of cells all round the embryo. In specimen III on the other hand, the regularity of the basal trophoblast is a feature of the whole circumference of the placenta.

The fingerlike, trophoblastic papillae consist of cells which are similar to those of the more regular parts of the basal trophoblast, and also have vesicular nuclei. It was noticed in some sections cut through the anterior end of the placenta that clusters of these trophoblastic cells could be seen lying completely within the enlarged capillaries in the decidua compacta and yet apparently having no effect on their walls. A few such cells can be seen within a capillary in Pl. VII, Fig. 34. Plate X, Fig. 46 represents the same transverse section cut through this area of the placenta and shows the initial contact of the trophoblast with the degenerating uterine epithelium, as well as the penetration of the trophoblastic papillae into the lacunae. In some parts the walls of the lacunae are intact as in Pl. VII, Fig. 34, but in others the endothelial lining of the enlarged capillary has been completely destroyed and what was the lumen of the vessel is completely filled by cellular trophoblast. By studying the serial sections it could be observed that the initial penetration of the blood-vessel takes place immediately below the uterine epithelium where this has been destroyed by the proliferating basal trophoblast. A tuft of these cells then grows into the lumen of the blood-vessel and only after it has become

established there is the endothelial wall of the vessel destroyed. Hence at the tip of any such trophoblastic projection, which has pushed its way into a vessel, the trophoblast cells may be seen in four or five consecutive sections lying in the lumen of the vessel but apparently having no effect on its wall as in Pl. VII, Fig. 34. For the rest, however, by following the length of the papilla the original course of the blood-vessel up to its nearest point to the uterine epithelium can be traced, although its endothelial wall has been destroyed. This may cover 12 or 13 sections.

As has already been mentioned, these trophoblastic papillae are not found round the equatorial zone of the placenta. In this region, instead, the basal trophoblast, on coming in contact with the much enlarged inner end of a vessel, is flattened against its endothelial wall. This it eventually destroys so that maternal blood continues to pour into and out of the foetal lacunar system. Nevertheless the course of the maternal venous and arterial blood through the foetal part of the placenta cannot be conclusively ascertained from this specimen.

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SPECIMEN VI.

A. Maternal tissues.

Uterine epithelium.

The structure of the uterine epithelium in the different parts of the uterus is similar to that already described in specimen V. In the implantation area this layer of cells has again been completely destroyed.

Stroma.

In the non-implantation zones the distribution of the different stromal tissues is the same as that pictured in Pl. IX, Fig. 42. In this uterus, however, the aggregations of brown pigmented material which were not found in the uterus of specimen V, are very numerous and scattered throughout the endometrium. Nearer to the implantation site, however, these bodies are confined to the outermost one-third of the stroma just below the myometrium as they were in specimen III.

In the vicinity of the attached embryo the same changes were noticed as those already described in the stroma of specimen V. Stromal oedema has encroached on the outer, denser connective tissue at the periphery and the decidua compacta is in the process of formation in the area where the initial penetration of the basal trophoblast takes place. In describing the decidua compacta of a uterus with a uterine swelling of 15 mms. in diameter, THURSBY-PELHAM (1924) mentioned how its cells changed in character as the foetal side was approached. The same variations are noticeable even in

this earlier stage. Thus on the side of the decidua compacta nearer to the myometrium, the cells are spindle-shaped with small, oval, darkly staining nuclei. Nearer to the trophoblast the cells become irregular in outline and their nuclei are much larger. Such nuclei are round, pale in colour and contain a few chromatin granules. In most cases each nucleus shows one distinct nucleolus. Scattered among such cells are some uninucleate predecidual cells, a great number of polymorph leucocytes and considerable quantities of blood extravasates (Pl. XI, Fig. 50). It should be noted that this uterus, with a uterine swelling which measures 8 mms. in diameter, is the only one so far described in this paper, in which blood extravasates could be identified lying between the stromal cells. Finally, as in specimen V, in that part of the decidua compacta in contact with the advancing basal trophoblast the cell boundaries are no longer distinct. In this area large decidual cell masses, some of them multinucleate and some uninucleate, occur. In addition, these irregularly shaped cell clusters contain numbers of inclusions, some of them small, others large, but all lipo-protein bodies which are known to occur in the animal body where great changes in metabolism are in progress.

An interesting feature which is clearly illustrated in the uterus of specimen VI, although not very obvious in specimen V, is the distribution of this congested decidual tissue. Observations show that such tissue is well developed only at the points where the fingerlike projections of the trophoblast are actively penetrating the tissue of the mucosa, i.e. at the two poles. The extent of the decidua compacta is, therefore, not uniform but tends to be greatest where the basal trophoblast is making the deepest inroads on the uterine tissue. In those sections, however, in which the amnio-embryonic vesicle is present, the dense region of the decidua compacta is no longer clearly demarcated although decidual giant cells and degenerating stromal tissue can of course be seen in the innermost zone of the endometrium adjacent to the basal trophoblast. This basal trophoblast round the equatorial region is thrown into rather irregular folds (Pl. II, Fig. 10). The clusters of degenerating maternal cells

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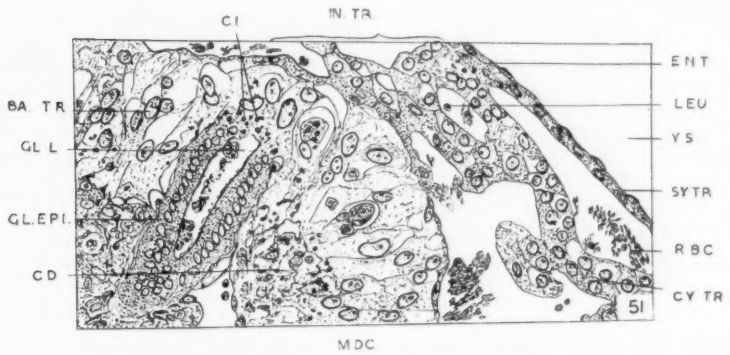
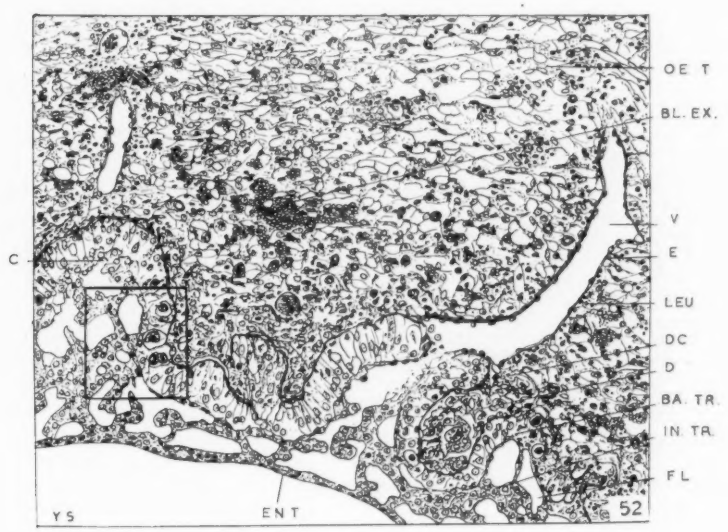
PLATE XII.

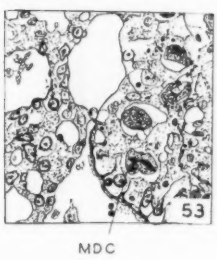
Fig. 51. Shows part of the foetal-maternal border of specimen VI. Note the penetration of the basal trophoblast into a gland lumen, the cell debris lying just below the basal trophoblast and the decidual giant cells and cell inclusions in the trophoblast. × 240.—Fig. 52. Shows part of the implantation area of specimen VI. Note the irregular arrangement of the basal trophoblast to form crests and depressions. The decidual tissue and cell debris is lying within the depressions. Two veins are present which obviously pierce through those parts of the basal trophoblast which cover the crests of the trophoblastic folds. × 90.—Fig. 53. Shows an enlargement of the area of the trophoblast which is outlined in Fig. 52 and illustrates the presence of decidual giant cells engulfed by the trophoblast. × 180.—Fig. 54. Shows the peripheral arrangement of the nuclei in the multinucleate giant cells found in specimen VIII. Note that two of these cells shown here have already been surrounded by the basal trophoblast. × 240.

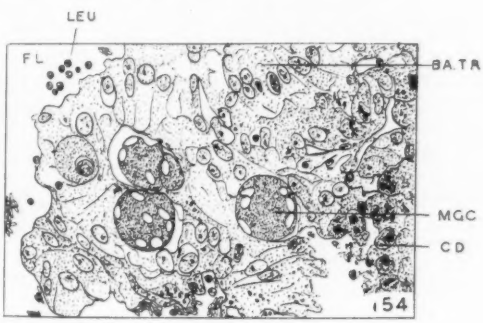
THE EARLY EMBRYOLOGY OF PROCAVIA CAPENSIS

PLATE XII.









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and the decidual giant cells are mainly found lying in the depressions between such folds (Pl. XII, Fig. 52). It is, however, the sections cut through this equatorial plane which show the greatest concentration of blood extravasates, these being present between the oedematous cells of the stroma, at the fringes of the basal trophoblast (Pl. XII, Fig. 52). The oedema is so intense in this area that the tissue has a homogeneous, pale pink appearance, except for its punctuation here and there by clear rounded spaces. In this zone there are numbers of polymorph leucocytes. The endometrial cells have small, rounded nuclei.

This uterus, therefore, shows clearly that the uterine mucosa undergoes the change involving the formation of decidual cells prior to its invasion by the trophoblast. Then by degrees all this decidual tissue is engulfed by the basal trophoblast. Thus in those regions, viz. in the equatorial plane, where the embryonic vesicle is attached, and where the foetal placenta is already well-established, the uterine mucosa has been encroached upon and destroyed over a considerable area. In such parts the decidua compacta has, therefore, been very largely replaced by foetal tissues, so that it is only the outer oedematous region of the endometrium which is still intact.

There is ample evidence that the giant cells which in some places can be seen within the borders of the basal trophoblast (Pl. XII, Figs. 51 and 53) are, in reality, maternal decidual cells of stromal origin. Similar cells can be seen as deeply stained masses at the foetal maternal border. When engulfed by the trophoblast they seem to be more resistant than other cell debris which is taken in, and consequently lie within the basal trophoblast for some time before they are absorbed. Describing the placenta associated with an embryo of 16 mms. crown-rump length, WISLOCKI and VAN DER WESTHUYSEN (1940) noted in referring to such giant cells: "These degenerating multi-nucleate masses are more abundant at this stage in the decidua of the polar regions than beneath the placenta proper." This present investigation confirms this. However, in specimen VI, a considerably younger stage than that referred to in WISLOCKI and VAN DER WESTHUYSENS' description, only a very few of these giant cells show the peripheral arrangement of the nuclei mentioned by them. In the majority of the giant cells in specimen VI the nuclei still have a haphazard arrangement. The facts that these giant cells are more common in the polar regions of the placenta in specimen VI and that the decidua compacta shows the strongest development in these areas, give added weight to the views held by both PELHAM (1924) and WISLOCKI and VAN DER WESTHUYSEN (1940) that "the multinuclear 'giant cells' seen at the fetal-maternal border are of decidual origin".

Glands.

These again show a resemblance to those found in specimens III, IV and V. However, in this uterus it is of interest to note that even in those parts of the uterine wall associated with the equatorial part of the placenta, a few straight ducts of the glands could be found passing through the endometrium to its foetal side. The openings of such ducts are blocked by cells of the basal trophoblast (Pl. XII, Fig. 51). Therefore, any secretions still being produced by these few remaining glands can be absorbed directly by the foetal cells.

Blood-vessels.

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The most noticeable difference between the blood supply in this specimen and that of specimen V is that the intense vascularization of the polar regions is no longer such a conspicuous feature. However, some maternal lacunae are certainly present and it is into these that the trophoblastic papillae make their initial penetration as previously described. Nevertheless, these lacunae are fewer in number and more widely distributed, so that the subepithelial area of the uterus at each pole does not have the appearance of a wide-meshed net as in specimen V.

In parts of the endometrium adjacent to the equatorial region of the placenta, the general arrangement of the blood-vessels is similar to that described in specimen V. However, although the placenta now occupies a greater area, the number of blood-vessels does not seem to have increased and consequently they appear to be more widely separated than in the younger stages. Veins are still more numerous than arteries, but the frequent branching of the veins, which is a characteristic feature of specimen V, is not found to the same extent here. In fact, very few of the enlarged, straight venous channels are inter-connected at the foetal-maternal border as in specimen V (Pl. XI, Fig. 47). The arteries are similar in form to those already described in the previous specimen.

One feature of special interest is, however, noticeable in connection with the penetration of the blood-vessels through the basal trophoblast. As already mentioned, the basal trophoblast is rather convoluted. Consequently in parts where this trophoblastic layer is folded out, the inner trophoblast consists of several rows of irregularly shaped lacunae, while below the depressed parts of the basal trophoblast hardly any lacunae are visible in the narrow zone of inner trophoblast in contact with it. The veins all leave the basal trophoblast covering the crests of such folds (Pl. XII, Fig. 52), while the arteries seem to lead into the depressions between the folds. None of the arteries, however, had entered the foetal side of the placenta.

B. Foetal tissues.

This specimen resembles specimen V already described in this paper and specimen III (Hyrax 5) described by THURSBY-PELHAM (1924) in having a "well-developed trophoblastic layer which is everywhere in contact with the uterine lining, both ends and sides." This layer is of fairly uniform thickness throughout, except at the two poles, where it consists of irregularly-shaped protrusions which are engaged in penetrating the maternal blood lacunae. This penetration occurs in much the same way as described in specimen V, except that here the trophoblast at the anterior pole, after breaking through the uterine epithelium, penetrates the mucosa for a considerable distance in the longitudinal axis of the uterus. Thus in sections cut through the anterior end, the uterine epithelium appears intact in 60 sections, although these sections show trophoblastic cells destroying the stromal tissue. It is clear that this invasion by the foetal tissue occurs in that part of the endometrium where the decidua compacta is best developed.

The trophoblast is again clearly differentiated into basal and inner trophoblast:

1. The basal trophoblast is represented by a single layer of deep columnar cells lying nearest to the maternal tissues. Especially at the two poles, but also in other parts of the placenta, the cells of this layer contain a number of inclusions, such as lipo-protein bodies, pycnotic nuclei and other cellular debris. These lipo-protein bodies are similar to the inclusions which have been described in the ectodermal cells and in the cavity of the amnio-embryonic vesicle in specimens IV, V and VI. This material has obviously been accumulated as the result of the phagocytic activity of the cells of the basal trophoblast. Maternal decidual cells can also be identified within the borders of this basal trophoblast (Pl. XII, Figs. 51 and 53). At the two poles mitotics are common in this layer. Between the two poles this basal trophoblast does not show the same development of papillae, but forms an undulating layer where it makes contact with the endometrium.
2. The inner trophoblast shows a greater thickness than in specimen V. It is delimited on the maternal side by the basal trophoblast and on the foetal side by a regular narrow layer of syncytial tissue with darkly stained, flattened nuclei. This thin layer of tissue is closely apposed to the yolk entoderm which completely lines the placenta except at the point where the amnio-embryonic vesicle is attached (Pl. II, Fig. 10). In this attachment stalk a few mesodermal cells form the contact between trophoblast and amnio-embryonic vesicle as already described earlier in this paper. This is illustrated in Pl. III, Fig. 13. Therefore, THURSBY-PELHAM (1924) was

wrong in her assumption that the layer of cells which lies closely apposed to the inner surface of the trophoblast was the mesoderm of the chorion.

Due to the convoluted form of the basal trophoblast, the inner trophoblast varies considerably in thickness being thicker in parts where the basal trophoblast protrudes and narrower where it is depressed (Pl. XII, Fig. 52). Everywhere, however, it consists of "a cellular network enclosing lacunae containing maternal blood" (THURSBY-PELHAM 1924). Except for its inner syncytial layer, it consists of cellular lamellae composed of polygonal cells with rounded, vesicular nuclei. In describing her specimen III which also showed a uterine swelling of 8 mms. diameter, THURSBY-PELHAM (1924) was able to differentiate this inner trophoblast into three zones according to the sizes of their lacunae. In my specimen having the same dimensions, it is difficult to identify this characteristic. In fact, in some parts of this area where the basal trophoblast is depressed, the lamellae of the inner trophoblast only enclose a single set of lacunae. However, in parts where the basal trophoblast is folded out and the lacunae are more numerous, there is some indication that lacunae on the maternal and foetal sides are larger than those which are enclosed by the more compact network of the middle region. This is, however, a feature which is much more characteristic of older specimens. All these lacunae contain maternal blood which includes many leucocytes. At this stage of pregnancy there is still no development of foetal blood-vessels.

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SPECIMEN VII.

As was mentioned in the earlier part of this paper dealing with the embryology, this specimen is badly preserved. Of all the uteri which were sectioned, this is really the only specimen in which the state of preservation is such that accurate histological investigation is impossible.

However, even in this series, it is possible to identify the distribution of the oedema and decidua compacta, the course of the blood vessels and the extent of the basal and inner trophoblast. In all these matters and in the general form of the developing placenta, this specimen shows no appreciable difference from the structure of specimen VI which has already been described.

SPECIMEN VIII.

A. Maternal tissues.

Uterine epithelium.

Both in the non-implantation areas and at the poles of the attached embryo, this tissue shows the same structure as in specimens previously described. It has been completely destroyed at the implantation site.

As in specimen III, the uterine lumen in front and behind the attached embryo is filled with blood extravasates.

Stroma.

The condition of the stroma in the non-implantation areas is the same as in specimens V, VI and VII. The same reactions by the stromal tissues to the penetration of the trophoblast can also be observed. These changes include:

1. The formation of oedema in the inner-most half of the endometrium.
2. The accumulation of polymorph leucocytes in this area.
3. A decidual reaction which supersedes the oedema in areas in immediate contact with the proliferating trophoblastic papillae especially at the poles. It is in these polar areas that the most conspicuous difference occurs between this specimen and those previously described.

In younger stages, the majority of the decidual cells are uninucleate ones although some larger cell masses can be found at the foetal-material border. In this uterus of specimen VIII, however, multinucleate giant cells are much more in evidence. Some of these are round in form and show a peripheral arrangement of their nuclei (Pl. XII, Fig. 54). In many cases, on the other hand, these structures have become very large and consist of a greater amount of cytoplasm and more nuclei than the giant cells which occur in specimen V. It is possible, therefore, that these are more of the nature of syncytial masses than single giant cells. Although describing relatively older uteri, THURSBY-PELHAM (1924) and WISLOCKI and VAN DER WESTHUYSEN (1940) also noticed that the quantity and size of the decidual syncytial masses or giant cells increases as pregnancy advanced. Many of these giant cells can be seen lying within the trophoblastic tissue as well.

Such a decidual reaction is again most conspicuous at the two poles of the blastocyst. Between these two poles decidual cell material is lying mainly in the depressions formed by the folding of the basal trophoblast as in specimen VI, but in these areas the tissue is obviously undergoing disintegration.

Blood extravasates are even more abundant in the stroma than in the previously described uteri. They are especially plentiful round the equatorial part of the implanted embryo, where in some places the basal trophoblast appears to be completely covered by extravasates. Such material consists mainly of red blood corpuscles but also contains a high proportion of polymorph leucocytes and quantities of fine brown granules, which are probably blood pigment. This brown granular material also occurs in some of the foetal lacunae and in the cells of the inner trophoblast, especially at the innermost foetal border of the placenta. It has not been found in younger stages but WISLOCKI and VAN DER WESTHUYSEN (1940) noticed a dark deposition of iron pigment in the syncytium lining the innermost blood lacunae of the

placenta associated with an embryo of 16 mms. crown-rump length. They suggested that it might be an artifact produced by formalin fixation. As the uteri at present under discussion were definitely not fixed in formalin, I am inclined to agree with their second alternative, viz. that "it is of a physiological rather than of an accidental nature."

This brown pigment is not the same in form or appearance as that which constitutes the aggregations of brown material which have been mentioned in most of the other specimens so far described and which also occur here. They are located mainly in the peripheral parts of the endometrium below the uterine muscles. These last-named bodies are more in the nature of histiocytes which are loaded with fat and brown pigment, and are products of a previous pregnancy.

Glands.

As in specimens V, VI and VII, glands only form conspicuous constituents of the uterine wall in the non-implantation areas. In such parts of this uterus their lumina are filled with secretions. But at the implantation site they are small and inconspicuous and obviously non-functional.

Blood-vessels.

These are very similar to those already described in specimen VI. The network of enlarged maternal vessels, which was so characteristic of the polar regions of specimen V, is again present but is less extensive and in this respect resembles the arrangement in specimen VI.

Between the two poles, veins are still more plentiful than arteries. These veins follow the same course as in previous specimens but do not appear to branch so much near the basal trophoblast, as in specimen V. However, they do dilate at their innermost ends and can be identified opening through the basal trophoblast from the outermost, large, foetal lacunae just beneath this layer. Arteries also occur but still appear to be a less conspicuous feature than the veins. This is due partly to the fact that they do not become enlarged at the foetal-maternal border. Several such arteries were traced through the endometrium but in no instance could they be found breaking through the basal trophoblast or opening into the foetal lacunar system.

In the light of what happens at a later stage of pregnancy, it is of special significance to notice that these arteries, in the equatorial plane of the placental area, seem to be un-affected by the basal trophoblast. In this specimen VIII, it seems clear that the supply of maternal arterial blood to the trophoblastic lacunae is mainly achieved by the penetration of the maternal lacunae at the two poles of the placenta. It is only later, when the maternal lacunar system is completely reduced, that the basal trophoblast begins to attack these arteries in the equatorial zone.

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B. Foetal tissues.

The placental area still exists all round the embryo, the trophoblast being more or less the same thickness at the two poles as in the equatorial region. Thus the characteristic zonary placenta, which has been described for older stages, is not yet apparent in this specimen which shows a uterine swelling of 9 mms. diameter.

Penetration by the fingerlike trophoblastic papillae into the decidua compacta and its maternal blood-vessels occurs as in specimens V, VI and VII. After the uterine epithelium has been destroyed, these outgrowths penetrate through the endometrium in the longitudinal axis of the uterus. Thus, as in specimen VI, at the two poles of the blastocyst a number of sections in the series show the trophoblastic tissue spreading through the endometrium although the uterine epithelium is intact. It is in these regions that the maternal, multinucleate giant cells are so conspicuous (Pl. XII, Fig. 54).

The placental area still consists of basal and inner trophoblast. It has increased in thickness and is now almost as thick as the remaining part of the endometrium, with which it is in contact. The basal trophoblast consists of large columnar cells. It follows a rather more irregular course than in specimens VI and VII, probably due to its deeper invasion of the uterine tissues. In the previously described specimens it was undulating but the corrugations were more or less regular. In this specimen many of the crests of the folds are drawn out into lobulate papillae which may push into the endometrium not only in a radial direction, but may turn and run parallel to the rest of the basal trophoblast for a short distance. Pl. XIII, Fig. 55 shows such a lobule cut in transverse section. The folds and depressions are more pronounced, not only at the poles, but also in the equatorial region of this placenta, than they are in specimens VI and VII.

The inner trophoblast is definitely thicker than in any of the other specimens so far discussed. The cell structure of its network of lamellae is, however, similar. The number of small foetal lacunae in the middle zone of the inner

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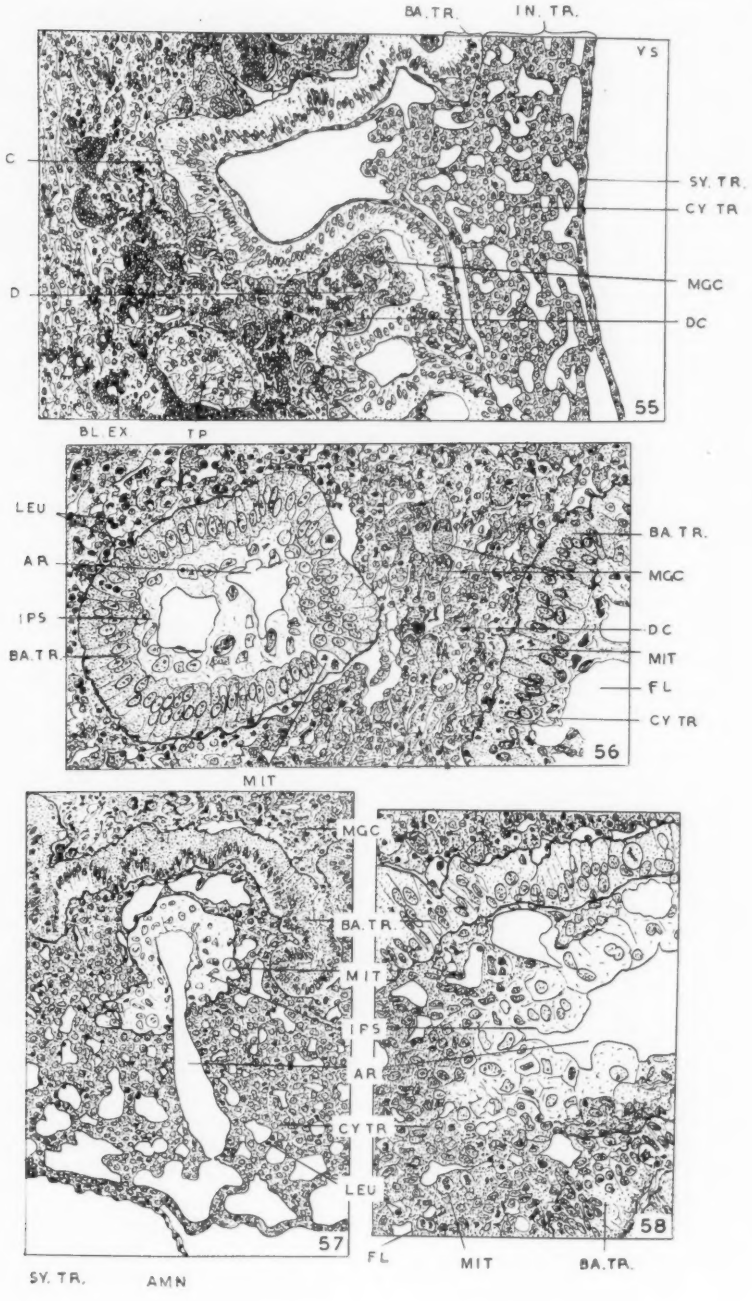
PLATE XIII.

Fig. 55. Shows part of the trophoblast and adjacent stroma of specimen VIII. Note the variations in the size of the foetal lacunae, the largest lying just below the basal trophoblast. On the left a trophoblastic papilla which was running parallel to the basal trophoblast has been cut. × 90.—Fig. 56. A transverse section of an artery lying in the endometrium of specimen XI. Note the structure of its wall which consists of an outer layer of basal trophoblast and inner, syncytial peri-arterial sheath. × 180.—Fig. 57. Shows a maternal artery passing through the inner trophoblast and opening into a foetal lacuna on the foetal side of the placenta in specimen XI. Note the absence of endothelium. × 90.—Fig. 58. Shows the continuity of the cells of the inner peri-arterial sheath of the artery with the cytotrophoblast and their possible derivation from it in specimen XI. × 180.

PLATE XIII.



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trophoblast has, however, increased and the gradations in the size of these lacunae from basal trophoblast to the innermost edge of the lacunar trophoblast has now become visible. The lacunae just within the basal trophoblast are enormous and most are filled with blood which makes them even more conspicuous. In many cases where the basal trophoblast has pushed outwards into the endometrium, the whole bulge is occupied by such a large lacuna. It is from these lacunae that the dilated venous channels leave the foetal placenta. The relatively more extensive middle part of the inner trophoblast, however, is occupied, as already mentioned, by numerous smaller lacunae. These also contain some maternal blood, including quite a number of polymorph leucocytes. In this specimen, however, even these lacunae are much larger than those occurring in the same area of the inner trophoblast in specimen XI. Finally, the innermost lacunae on the foetal side of the placenta are again somewhat larger than those in the middle zone, but they are definitely not as large as the outermost lacunae. These innermost lacunae are enclosed by a thin syncytial tissue and not by the wider cytotrophoblastic tissue which surrounds the smaller lacunae.

The mesoderm of the chorion has not yet developed and there are no foetal blood-vessels. The thin layer of tissue which lines the inner trophoblast is, therefore, for the greater part, the yolk entoderm.

SPECIMENS IX AND X.

Although the embryos contained within these uteri are at different stages of growth, the condition of the developing placenta in each case is almost identical. In this respect, moreover, they show very little advance on the structure of the placenta as described in specimen VIII. The main changes which have occurred are as follows:

A. Maternal tissues.

1. The peripheral part of the endometrium lying below the muscles, which in previous specimens was mainly of an oedematous nature, is now composed very largely of fibrous connective tissue.
2. The decidua compacta is a conspicuous feature, especially at the two poles where it includes a great number of multinucleate giant cells. Cellular debris, pycnotic nuclei and decidual cell masses can, however, be found in small quantities in all parts of the placental area, at the foetal-maternal border. Blood extravasates and polymorph leucocytes are still noticeable constituents of the stroma.
3. The maternal lacunar system at the poles is no longer well-developed. In fact, although maternal vessels occur in these areas and are still attacked by the trophoblastic papillae, none of them appear to become enlarged.

4. In the zone between the two poles a few arteries could be seen penetrating right through the trophoblast to the large lacunae on the foetal side of the placenta. The structure of their walls and their method of entry into the foetal tissues, can, however, be much more clearly observed in specimen XI, and I shall, therefore, deal with this histological description in the next section of this paper.

B. Foetal tissues.

The most striking advance which these two specimens, IX and X, show is in the appearance of the first foetal blood-vessels. However, there is no allantois, so that these blood-vessels are all vitelline vessels and are found in the splanchnic mesoderm as shown in Pl. IV, Fig. 18. Even the splanchnopleure has not yet developed completely, so that foetal blood-vessels are confined only to the region of the placenta in the neighbourhood of the embryo proper. It is, therefore, only in this area that a chorio-vitelline placenta can be said to have developed. At the abembryonic pole it is still a non-vascular yolk-sac placenta. The placenta, nevertheless, continues to be circumferential and there is no appreciable difference yet in the thickness of the trophoblast in the polar and equatorial regions.

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SPECIMEN XI.

This specimen has a uterine swelling with a diameter of 12 mms. and contains a 27-somites embryo. Although this embryo is considerably older than that of specimen X, there is still no indication of the development of the allantois.

A. Maternal tissues.

The outstanding characteristics of the uterine tissues of specimen XI when compared with all other specimens so far described are referable to two features. These are:

1. The multinucleate giant cells of the decidua compacta.
2. The structure of the arterial walls, and the method of penetration of the arteries through the trophoblast.

Multinucleate giant cells are now particularly abundant. The majority of such cells show the peripheral arrangement of the nuclei which WISLOCKI and VAN DER WESTHUYSEN (1940) described as being so characteristic of older stages. Just in front and behind the trophoblastic papillae which are invading the polar areas, the decidua compacta continues to be a conspicuous feature, consisting at this stage of pregnancy almost entirely of a solid mass of such multinucleate giant cells. However, such giant cells are also becoming increasingly numerous throughout the placental area. Many of them can be identified at

the foetal-maternal border even in the equatorial zone of the implantation area. This is not the case in the younger specimens already described where the multinucleate giant cells are very largely confined to the polar regions.

At the poles a few large vessels occur in the stroma and are penetrated by the trophoblast, but the maternal lacunar system is again lacking as in specimens IX and X. It has, therefore, become necessary for the supply of arterial blood to reach the foetal lacunae in some other way. This is achieved by the pushing of arteries through the trophoblast to the foetal side of the placenta. Such penetration by the arteries may now take place at any point in the placental area, but more arteries can be identified passing through those parts of the trophoblast which are in the neighbourhood of the embryonic disc than elsewhere.

Maternal arteries were found converging in the basal trophoblast but not opening through it in specimen VIII. The way in which the arterial wall is destroyed and eventually replaced by a continuous layer of trophoblastic cells is especially interesting and is well illustrated by a study of specimen XI. On examining serial sections, the first significant feature to be noticed is that cut parts of maternal arteries even some distance from the basal trophoblast, lying in the endometrium, are each surrounded by a sheath of trophoblastic cells as shown in Pl. XIII, Fig. 56. Such arteries can then be traced into the foetal lacunar system. Each one passes through that part of the inner trophoblast which encloses very tiny lacunae, and opens directly into one of the larger lacunae at the foetal side of this placenta (Pl. XIII, Fig. 57).

The structure of these arteries is noteworthy. Mention was made of this by WISLOCKI and VAN DER WESTHUYSEN (1940). In describing the structure of the arterial walls in uteri containing embryos which are older than this specimen XI, they mentioned that: "The trophoblast encases the arteries almost down to the layer of uterine muscle." Then they described the periarterial sheath as consisting of an outer layer of columnar basal trophoblast and "an inner periarterial sheath composed of rather clear cells with fairly distinct boundaries." Lining the lumen of the artery were remnants of the endothelium and "an indistinct lamina of reticular connective tissue comprising remnants of the former intima," but in many cases these were found to be lacking. The arteries in specimen XI show clearly the presence of the outer layer of columnar, basal trophoblast cells and the inner periarterial sheaths, but in most the endothelium was lacking (Pl. XIII, Fig. 56). This inner sheath is most conspicuous in the wall of the artery where it enters the zone occupied by the lacunar, inner trophoblast. In this area it is almost as thick as the basal trophoblast. Here, too, its cell structure is much more distinct than in the part of the artery which is in the endometrium, where it is almost syncytial in nature. Its cells are large, consisting of a mass of non-granular cytoplasm and a rather irregularly-shaped vesicular nucleus. This inner, periarterial sheath

round that part of the artery which lies in the endometrium, however, rarely shows distinct cell boundaries and is not so extensive as elsewhere (Pl. XIII, Fig. 56). About half-way through the lacunar trophoblast even this inner sheath of the arteries is lost, so that that part of the artery which penetrates through to the large lacunae on the foetal side of the placenta, is surrounded only by a layer of cytotrophoblast which forms its wall (Pl. XIII, Fig. 57).

The veins have the same structure and show a similar method of exit from the foetal lacunae on the maternal side of the placenta, as they have done in all other specimens so far described.

B. Foetal tissues.

The placenta continues to be circumferential in form. Although the embryo is considerably advanced in its development when compared with specimen X, the allantois has not yet made its appearance. Therefore the foetal blood-vessels which are found associated with the placenta round the embryonic pole are still vitelline vessels. There is, moreover, an area at the abembryonic pole in which even vitelline vessels are lacking.

The most noticeable change in the structure of the foetal tissues is referable to the formation of the inner or lacunar trophoblast. In previously described specimens, viz. IX and X, the lacunae in the middle region of the inner trophoblast were smaller than those on either side of it. In this specimen there has been an even further reduction in the relative size of these lacunae. The cytotrophoblast in this area now appears as a denser labyrinthine meshwork than before, which results in a corresponding reduction in the size of the lacunae formed by it. Consequently, the size of the lacunae just below the basal trophoblast and those which are enclosed by the syncytial trophoblast at the foetal side of the placenta, appear by comparison to be much larger and more conspicuous than those in the middle region (Pl. XIII, Fig. 57).

The appearance of the basal trophoblast is also somewhat different. Its cells are not quite so tall as before. Their nuclei are more basally placed, so that those parts of the cells lying nearest to the endometrium are occupied only by clear cytoplasm of a homogeneous pink appearance after staining (Pl. XIII, Fig. 57). Mitotics are still common in this layer, but its phagocytic activity seems to have been somewhat reduced as little cellular debris was noticed in its cells.

SPECIMEN XII.

This specimen consists of a part of the uterus which shows a swelling 14.5 mms. in diameter and contains a 48-somites embryo. Embryonic development has proceeded to a much greater extent than in specimen XI and the

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allantois is now a conspicuous feature. The yolk-sac has been correspondingly reduced but is now vascularized all round.

The placenta is, however, still circumferential and the trophoblast consists, as in specimen XI, of basal trophoblast and inner trophoblast, the latter being composed of cytotrophoblast and syncytiotrophoblast. Where the allantois is in contact with the trophoblast it is beginning to form tiny foetal villi. It is richly supplied with blood-vessels.

In all essential details, therefore, this specimen conforms to the description which was given by THURSBY-PELHAM (1924) for her specimen which showed an uterine swelling of 15 mms. diameter. It is also very similar to WISLOCKI and VAN DER WESTHUYSENS' specimen at limb-bud stage. Thus it provides the stage at which this present investigation links up with other work previously carried out in connection with this animal, Procavia capensis, in regard to its placentation.

DISCUSSION.

Non-pregnant uteri.

The preliminary work on the three non-gravid uteri described in this paper has not been sufficiently thoroughly done to warrant definite conclusions being drawn with regard to the form of the oestrous cycle found in Procavia capensis. It has, however, opened up an interesting field which should yield valuable information, when it is more carefully examined and use is made of the vaginal smear technique to supplement observations made on the structure of the uterus and ovary.

From my limited observations, I would suggest that Procavia is a polyoestrous animal and that there is very little rest period between successive oestrous cycles. The first uterus described viz. the dioestrous uterus, is definitely in a condition engendered by the absence of fertilization, for it shows certain features in common with the oestrogenic uterus. These are the swollen uterine epithelium, the presence of stromal oedema and the abundance of polymorphonuclear leucocytes. The ovary, moreover, contains well-developed corpora lutea. At the same time, however, the uterus also shows degenerative changes, especially in the subepithelial, stromal cells. Mitotics are, moreover, few in number.

The second non-gravid uterus described here shows the link between these degenerative changes and the beginning of the next oestrous cycle. If the interpretation of the phases in the oestrous cycle given by PARKES (1929) be followed, it seems reasonable to suppose that Procavia substantiates his view that "The polyoestrous animal ... with a series of cycles in a breeding season enters upon a transitory period of development, the dioestrous interval. At the end of this short phase proestrus supervenes and the cycle starts again."

Furthermore, in some animals like the guinea pig, dioestrus is really pseudo-pregnancy and it has been observed that "In animals such as the guinea pig with a dioestrous cycle containing a luteal phase, the end of the latter (viz. pseudo-pregnancy) is rapidly followed by proestrus" (PARKES 1929).

In Procavia, however, the collection of material over a period of several years has proved fairly conclusively that, even if a polyoestrous animal, Procavia capensis has only one pregnancy year. VAN DER HORST (1941) explained that the length of the gestation period of this animal is probably 6 to 7 months. This inference was made after supervising the collection of the material, some of which has been used for this present investigation. This supervision showed that by November or December of any year the embryos are near birth, while in the intervening months the gradual growth of the embryos could be traced. In order to collect uteri which showed no outward signs of gravidity and yet contained the youngest embryos, the work had to be started as early as April. Support for this view has been given by MURRAY (1942) who gave the period of gestation of Procavia as 225 days. It is interesting, moreover, to note that more recently WEBB (1946), in describing the birth of a Tree Hyrax (Dendrohyrax arboreus crawshayi) in the London Zoological Gardens, gave reason to believe that this animal also has a relatively long gestation period. He mentioned that this Tree Hyrax showed an advanced state of development at birth. Many of its features, for instance its relatively large size in comparison with that of the mother, and the strong development of its lower incisor teeth, tended to suggest that it was capable of looking after itself almost immediately after birth. WEBB (1946) came to the conclusion, therefore, that the Tree Hyrax also has a long gestation period and that "this would account for the advanced state of development of the young at birth".

The data collected from a study of the histology of only the few non-gravid uteri described, together with the above information supplied by VAN DER HORST (1941), MURRAY (1942), and WEBB (1946) with regard to the length of the gestation period in the Hyracoidea, seem to indicate that Procavia normally has only one pregnancy a year. However, being a polyoestrous animal, should fertilization fail following the first ovulation, then another oestrous cycle follows and so on during the breeding season. It seems probable, therefore, that several ovulations may have to occur in Procavia before copulation and fertilization take place. Procavia thus provides an interesting contrast to the shrew, Blarina brevicauda Say, in which animal PEARSON (1944) has shown that many copulations are necessary before ovulation will take place.

Glands.

It has been shown by many writers that the uterine glands undergo changes in form and structure during the different phases of the menstrual cycle and

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at different stages of pregnancy. Procavia is no exception to this. The actual shapes of the glands, however, seem to be rather characteristic for any particular species, and many different examples can be given to illustrate this. To take but three of them, Elephantulus, Man and Halicore dugong may be mentioned. In Elephantulus and in the human female, "in the early oestrogenic phase the glands become straight, the lumina are narrow and the cells are tall ... Just prior to ovulation the glands are slightly coiled but at ovulation this coiling disappears completely and the glands are perfectly straight" (VAN DER HORST and GILLMAN 1941). In the pregnant uterus of Halicore dugong, the mouth of the gland opens into the dilated part of the neck which then narrows and passes through the endometrium for a short distance as a straight unbranched tube. This then bifurcates and becomes tortuous, and each terminal branch ends with a closed rounded end (TURNER 1889). In Procavia the glands in each uterus studied showed their own pecularities. In the dioestrous uterus their lumina are small throughout and each gland consists of a bifurcated fundus, a loosely coiled body and a straight neck which opens into the uterine lumen. At proestrus the glands are somewhat similar but the body is more tightly coiled. The oestrogenic uterus shows a marked change in the fundus region, which now forms a conspicuous, much dilated chamber just below the myometrium. This was also observed by THURSBY-PELHAM (1924) in one of the non-pregnant uteri which she described. In the earliest stage of pregnancy studied, one in which the embryo is still an unattached morula, the glands also have characteristic features. The fundus region of each consists of a tightly coiled ball while the body and neck are cork-screwlike.

However, although the general form of the gland at each stage is characteristic for a particular animal, certain structural features may be found which are common to different animals. For instance, it has been observed that in Procavia, as in Elephantulus, mitotics become more numerous in the glandular epithelium at oestrus. It was noticed, too, that the nuclei of cells which were about to divide moved away from the basement membrane. This phenomenon is also encountered in Elephantulus, baboons, rabbits and in the human female. In addition, the epithelium, both glandular and uterine, of the oestrogenic uterus is characterised in both Procavia and Elephantulus by the migration of the nuclei from a basal position in the cells to a central or even distal position. This phenomenon has also been described in the human glands in the progravid phase of the menstrual cycle. (BARTELMEZ and BENSLEY 1932.)

Probably the most outstanding feature of the glands in Procavia is that, as soon as the blastocyst becomes attached, they become progressively reduced in size and number and take a less and less active part in supplying nourishment to the embryo. In the specimens described in this paper, they seem to reach their maximum development at the time when the unattached morula is lying in the uterine lumen. In all other pregnant uteri studied, they form an in-

conspicuous feature of the uterus in the implantation area. In only one uterus, that with a uterine swelling of 8 mms. diameter, could a few glands be seen lying in contact with the invading trophoblast. For the rest, they appeared in the sections only as cut pieces just below the myometrium. Such glands are obviously inactive for their lumina are small, their epithelium is composed of low, cuboidal cells, and their nuclei are irregular in shaped and pycnotic. Earlier workers have also commented on this feature. ASSHETON (1906), in describing a cross section of the uterus, showed that that part of the endometrium just below the myometrium contained "here and there a cross section of a gland cut transversely; but these occur very sparingly and are scattered fairly evenly all round." He came to the conclusion, moreover, that the layer of trophoblast and trophospongia which completely surrounds the embryo would cut off any secretion which might be produced by the glands and, therefore, that "the glands of the uterus of this animal take no further part in the nourishment of the foetus." WISLOCKI and VAN DER WESTHUYSEN (1940) made a similar observation about the glands found in the uterus enclosing an embryo at limb-bud stage. Of this they said: "It is obvious that in Procavia the glands by this stage at least play a relatively insignificant role in the formation of the placenta." THURSBY-PELHAM (1924) made similar comments about her specimen which showed a uterine swelling of 8 mms. diameter. My investigation has now shown, not only that the glands play a relatively insignificant role in the development of the placenta, but also that the deterioration of these glands sets in as early as the time of implantation.

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This must be regarded as an outstanding and peculiarly characteristic feature of Procavia when this animal is compared with others placed in such widely divergent groups as Ungulata, Primates and Carnivora. In the sheep and pig, for instance, glands play an important role throughout embryonic development. In the dog, even before implantation, the glandular zone of the uterine wall is differentiated into a superficial part containing enlarged gland crypts and a deeper zone containing the narrower gland ducts. After implantation, with the enlargement of the embryonic vesicle, the glands form an integral part of the so-called compacta and spongiosa and those parts of their epithelium nearest to the plasmoditrophoblast help to form the maternal symplasm (DE LANGE 1931). Even in the Primate, Tarsius, the neck portions of the glands enlarge and their epithelium thickens as soon as the blastocyst is attached. Ultimately at the placental site, these epithelial cells form a syncytial mass which obliterates the glandular lumen, these syncytial clusters being placed at the fringes of the tropho-placental mass. It is clear then that in the majority of animals, except Procavia, the uterine glands play an integral part in supplying nourishment to the embryo, and may even assist in the formation of the placenta by preparing for the invasion of the trophoplast.

Changes in the endometrium-decidua and giant cells.

Conspicuous changes in the structure of the endometrium can also be traced as pregnancy advances. These are especially related to the distribution of the oedema, to the formation of the decidua compacta and to the appearance of giant cells. In describing the oestrogenic uterus of Elephantulus, VAN DER HORST and GILLMAN (1941) noticed that "the first evidence of commencing oestrus can be seen by the appearance of the oedema in the deepest part of the stroma where it lies in contact with the inner layer of muscle." Furthermore, after ovulation this oedema was observed to diminish first in the more superficial parts of the endometrium and later in the more deeply lying areas, so that "at one stage, the stroma consists of a superficial compact zone and a deep oedematous zone." In Procavia the oestrogenic uterus also shows an abundance of this uterine oedema. It is especially interesting to note, moreover, that in the pregnant uteri, the distribution of this oedema seems to depend on the proximity of the particular part of the endometrium to the implantation site. Thus at the two poles of the attachment area the endometrium consists of an inner zone of oedematous tissue nearer the lumen and an outer area of denser connective tissue below the muscles. Those parts of the endometrium in closer proximity to the blastocyst, however, show the gradual encroachment of oedema over a wider and wider area until it extends right through the width of the endometrium. Simultaneously, however, those tissues which become filled with fluid first, i.e. those nearer to the uterine lumen, start to show a decidual reaction.

MOSSMAN (1937) maintained that it could be proved that degenerative changes in the uterine epithelium, prior to its destruction by the trophoblast, were as much due to endometrial changes below it, as to the actual attachment of the trophoblast. In his words "epithelium does not degenerate until its blood supply is interfered with by some change beneath it usually edema." He found support for this hypothesis in the condition seen in the chipmunk, Tamias striatus. In this animal there are a number of abembryonic trophoblastic "attachment cones" but it was found that only some were associated with degenerative changes in the uterine epithelium. Further study revealed that degeneration of the epithelium in such areas was always associated with subepithelial oedema. In Procavia attachment is not localised but takes place all round the blastocyst so that the whole of the epithelium is eroded away in this area. It is significant that the oedema in Procavia is likewise not localised but occurs all round the uterine lumen, at the implantation site. This seems to support MOSSMAN'S view, although of course the effects of the trophoblast on the uterine epithelium as well cannot be ignored. It is of interest, however, to note that Procavia, like the chipmunk, kangaroo-rat, mouse and pocket-gopher, shows a distinct relationship between these two phenomena of epithelial de-

generation and subepithelial oedema. It should be mentioned that in Procavia the degeneration of the uterine epithelium simply involves the vacuolation of the cells and their fragmentation, while the nuclei become pycnotic and move away from the basement membrane. There is no thickening of individual cells nor the concentration of their nuclei in darkly staining heaps, as is the case in the macaque (WISLOCKI and STREETER 1938). The syncytial masses of uterus and glandular epithelium which are commonly seen in the early stages of placental development in animals like the squirrel and rabbit as well as some Carnivora and Primates are not found in Procavia either. Such syncytial, epithelial degeneration, however, takes place in the above-named animal at the time when the developing chorio-vitelline or chorio-allantoic placenta contacts the uterine epithelium. In Procavia, the uterine epithelium is destroyed and a trophoblastic lacunar system formed long before even the chorionic mesoderm makes its appearance and certainly before the growth of the allantois is commenced.

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The decidual reaction in Procavia is also characteristic and commences early. Thus, even in the uterus surrounding the youngest blastocyst here described, predecidual cell formation could be seen in the middle-third of the endometrium. By tracing the growth of these cells through later stages of pregnancy, it could be demonstrated that these predecidual cells enlarge and become components of the decidua compacta. Some of them remain uninucleate while others become bi- or multi-nucleate and ultimately, in stages with uteri showing placental swellings larger than 10 mms. in diameter, many of them gave rise to multinucleate giant cells. Although some of these could be identified lying within the trophoblast, it is clear that all are of maternal origin. WISLOCKI and VAN DER WESTHUYSEN (1940) were inclined to this view after their investigation of only specimens containing embryos older than limb-bud stage. Their description of the location of the giant cell nuclei "in a rim at the periphery of the cells" has also been corroborated by a study of younger stages.

WISLOCKI and VAN DER WESTHUYSEN (1940) also noticed that there was an increase in the number of giant cells in the three stages which they described and also a variation in the regions of their distribution. The first appearance in any quantity of distinct giant cell-masses was noticed in the polar regions of my specimen at the later primitive streak-stage, but it was only in the specimen with 6—7 somites that the peripheral arrangement of their nuclei became definitely apparent. WISLOCKI and VAN DER WESTHUYSEN showed that in their first two stages giant cells "are most plentiful at the poles of the blastocyst where reduction of the placenta is taking place. By the beginning of the definitive stage they have become very abundant in the region of the zonary placenta" (1940). In all my specimens the placental area is still circumferential and there is no indication of a specialized zonary area. It is a noticeable feature that in these early stages the decidual reaction is most marked in areas where the trophoblastic papillae are actively penetrating the mucosa,

i.e. in the polar regions. Hence, it is not surprising that in these regions the decidual giant cells appear first and gradually become more abundant. However, my specimen containing an embryo with 27-somites shows that these decidual giant cells gradually become more numerous throughout the placental area and, as development proceeds, show a tendency to become more abundant, especially in the equatorial zone where the zonary placenta is later established, as was observed by WISLOCKI and VAN DER WESTHUYSEN (1940).

There is, however, no indication that the decidual reaction is associated with the blood-vessels, as is the case in animals like the rabbit (MOSSMAN 1926). There is, moreover, no decidual cell reaction in Procavia immediately below the muscles nor in the myometrium itself. It is definitely started with the predecidual reaction in the middle third of the endometrium, occurs throughout the implantation area of uteri in early stages of pregnancy, but later becomes especially concentrated in the polar zones. Small amounts of decidual tissue and degenerating subepithelial cells only are to be observed in the depressions formed by the irregular protrusion of the basal trophoblast, between the two poles in young stages.

No giant cells of trophoblastic origin, such as were found in many Rodentia (MOSSMAN 1937) can be identified in Procavia.

Blood-vessels.

Many difficulties were encountered by earlier workers on Procavia capensis to whom only uteri at fairly late stages of pregnancy were available. Such difficulties were especially related to the blood supply of the uterus and placental area. This present investigation has helped to elucidate some of these problems.

It is clear that, at the time of implantation, the maternal blood-vessels in the area all converge on the uterine lumen and, in the subepithelial zone, form a branched network of dilated capillaries which are filled with blood. The sub-epithelial area, therefore, has the appearance of a widemeshed net in which the lacunae are separated by strands of decidual tissue. In the uterus containing the very young blastocyst, this was the condition all round the implantation site. A similar intense vascularization of the endometrium associated with the attaching embryo has been observed in the macaque (WISLOCKI and STREETER 1938) and in other Primates. In slightly older specimens of Procavia, viz. those at the stage of the amnio-embryonic vesicle, this network of enlarged maternal capillaries is more localised and is confined to the polar regions of the embryo. It is noteworthy that it is in these regions that trophoblastic proliferation is most active and hence it is clear that it is by means of penetration of maternal capillaries in the polar regions that maternal blood enters and percolates through the trophoblastic lacunae.

The method by which these lacunae are penetrated by the fingerlike trophoblastic papillae seems to be peculiar to Procavia. It is well illustrated in the embryo associated with an uterine swelling of 6 mms. diameter. These trophoblastic papillae, after making the initial penetration of a blood-vessel, do not affect the wall of the vessel further until they have grown a considerable distance up the lumen of the vessel. Thus, instead of destroying the tissues of the blood-vessel as they grow, which is the usual procedure, the trophoblastic papillae complete their penetration into the lumina of the vessels and only then erode the tissues more fully.

Even in these early stages, veins can, however, be seen opening through the basal trophoblast in the more equatorial zones of the implantation site as well as at the two poles. Arteries on the other hand are only opened up in the polar regions, those in the equatorial region remaining as yet unaffected by the trophoblast.

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However, as pregnancy advances the maternal lacunar systems at the poles become a less and less conspicuous feature. On the other hand there appears to be an intensification of the blood supply to and from the equatorial zone of the placenta, a phenomenon which is directly related to the changing form of the placenta from a circumferential to a zonary type. Such a change only becomes clearly established in the embryo with 27-somites. Now, it has been observed that the proliferative activity of the trophoblast is greatest at the two poles. Growth of the embryo therefore proceeds in the direction of the longitudinal axis of the uterus more rapidly than it does in diameter. It may well be, as a result of this, that the same blood-vessels which originally supply the two poles later supply the equatorial zone of the placenta, because the growth of the embryonic tissue has resulted in the two poles becoming more and more widely separated. However, even if this is a possible explanation it is clear that these blood-vessels supplying the equatorial zone of older placentae are not as branched or as dilated as those supplying the poles of earlier embryos. This may be due to the fact that in older stages they are responsible only for bringing blood to or taking it from an already well established lacunar system, which in earlier stages has not yet appeared.

A study of the veins in the earliest stages of pregnancy has very largely served to substantiate evidence already put forward by earlier workers like Assheton (1906), Thursby-Pelham (1924) and Wislocki and Van der Westhuysen (1940). Assheton described the veins as vessels which were not lined by a syncytial layer and which opened into channels which were apt to run parallel with the columnar epithelium. Thursby-Pelham said "The other channels are bounded by a squamous endothelium with small, darkly-staining nuclei. They can be traced from the large blood-vessels which run parallel to the basal trophoblast in the decidua near the muscularis; they run obliquely through the decidua and pass through the basal trophoblast to open

directly into the lacunae just internal to this layer. They lose their endothelium as they pass through the basal trophoblast. They are probably the maternal veins." This present investigation has established this so-called probability as an actual fact. Even in specimens as young as that of the early amnio-embryonic vesicle, vessels to which THURSBY-PELHAM's description would apply in all details, were found. Such veins could be traced in all the uteri studied and in each one showed that their position was not localised, for they may open through the basal trophoblast at any point in the placental area. All are, however, much dilated as they approach the foetal-maternal border. In every case the veins opened from one of the large, outermost foetal lacunae just below the basal trophoblast. It is clear, moreover, that the wall of each such lacuna is formed by cytotrophoblast and that the basal trophoblast is nowhere in direct contact with the lacuna. The escape of venous blood only along the margin of the placenta is a characteristic which Procavia has in common with many other mammals. It has been observed to be the case in the human placenta by SPANNER (1936), in marmosets (Oedipomidas geoffroyi) by WISLOCKI and STREETER (1938) and in rodents by MOSSMAN (1926 and 1937).

The main controversies in earlier papers seem to have been associated with the description of the arteries. All workers were, however, agreed that the arteries passed right through the trophoblast and opened into lacunae on the foetal side of the primordial placenta. With this view I also agree. Thus Procavia is again similar to many other animals in the disposal of its maternal arterial blood directly to the foetal side of the placenta, a condition which also occurs in the marmoset (WISLOCKI and STREETER 1938) and in Centetes (GOETZ 1936).

In describing blood-vessels which both ASSHETON and THURSBY-PELHAM claimed to have a syncytial lining and which they called arteries, THURSBY-PELHAM (1924) said "These channels do not seem to arise from any large blood-vessels but from several small sinuses that appear as slits in the outer part of the decidua." The investigation of earlier stages has shown conclusively that the uterine arteries originate, as do the veins, from the large vessels running in the myometrium and not from sinuses as suggested by THURSBY-PELHAM. The two types of artery found in the uterus of Macacus rhesus by DARON (1936) and in Macacus brevicaudus and Pithecus fascicularis mordax by HERBERG (1935) could not be identified in Procavia. In the last-named animal there seems to be only one type of artery. Each of these leaves a main artery in the muscles, follows a much coiled course through the outer one-third of the endometrium and may also bifurcate before passing as a straight channel towards the placental area. It is interesting to note that even in early stages of pregnancy the walls of these arteries lose their muscularis on entering the decidua compacta. GOETZ (1936) reported a similar phenomenon in the arteries of Centetes of which he said "Die Arterie zeigt nämlich solange sie in

der Tunica muscularis verläuft, einen in keiner Weise atypischen Wandbau. Mit dem Eintritt in die unveränderte Mucosa aber, gehen ihr zunächst nur stellen-weise, dann jedoch vollständig, alle elastischen Elemente (vor allem die Elastica interna) verloren. Jetz zeigt die Arterie nur noch Endothel, zirkulare Muskulatur und eine kaum entwickelte Adventitia."

As long as the maternal lacuna system is well developed in the polar regions, arteries elsewhere in the placental zone remain rather small and inconspicuous. As was suggested previously the growth of the embryo in the direction of the longitudinal axes of the uterus may be responsible for the fact that the two poles become more and more widely separated so that the vessels which were originally supplying the two poles later supply the equatorial zone of the placenta. It is certainly true that in the specimen with a 27-somites embryo the basal trophoblast has started to flow round the maternal arteries. Moreover these arteries are most numerous in parts surrounding the embryonic disc and are very largely confined "to the middle region of the embryo swelling," a fact which was also observed by ASSHETON (1906).

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Both ASSHETON (1906) and THURSBY-PELHAM (1924) claimed that the arteries were enclosed by a syncytial lining and that "this syncytial layer appears to form a partial lining of the lacunae" (PELHAM 1924) but THURSBY-PELHAM indicated that in a specimen of 17 mms. uterine diameter this syncytial lining could not be traced for more than a short distance through the decidua on the maternal side of the basal trophoblast. Furthermore, in an older specimen with an uterine diameter of 31.5 mms., she mentioned that the basal layer of trophoblast followed the endothelium of the artery for a considerable distance through the decidua and in the other direction through the inner trophoblast. From her account it seems that she used the terms "Syncytial lining" and "the endothelium" of the artery synonymously because on one occasion she refers to it as "syncytial endothelium". WISLOCKI and VAN DER WESTHUYSEN (1940) have given a much more explicit description of the structure of the arterial walls and with this I am in agreement.

It is clear from a study of my younger specimens that, prior to the encroachment of the basal trophoblast on the maternal arteries, they remain in the decidua and show normal structure except that those parts of the arteries lying in the decidua have lost their muscularis, and their walls in such areas consist mainly of endothelium.

In specimens showing an uterine swelling 10 mms. or more in diameter, where the basal trophoblast has flowed round the arteries, in some cases almost up to the point where they leave the myometrium, the wall of each artery consists of an outer layer of basal trophoblast and an inner peri-arterial sheath. This sheath at points furthest from the inner trophoblast certainly appears to be syncytial in nature consisting of a large, clear mass of cytoplasm containing irregularly shaped, lightly staining nuclei. It is possible that this is the layer

to which THURSBY-PELHAM and ASSHETON referred as the syncytial lining. PELHAM, however, believed that this was of maternal origin and derived from the maternal endothelium. I am inclined, on the other hand, to support the view of WISLOCKI and VAN DER WESTHUYSEN (1940) who believed that it was of trophoblastic origin. This is substantiated by the fact that remnants only of the endothelium could be found, showing that most of it had been eroded or destroyed and could not, therefore, have given rise to a new tissue. Secondly, it can be definitely demonstrated that "in places the outlying clear cells can be traced by transition without obvious interruptions with the inner layer of reticulated cytotrophoblast," as noticed by WISLOCKI and VAN DER WESTHUYSEN (1940).

I could not find the basal trophoblast following the artery through the inner trophoblast for any great distance as suggested by THURSBY-PELHAM. The inner peri-arterial sheath does, however, line the artery for about half its length as it penetrates through this trophoblastic labyrinth. In the inner half of the labyrinth the arterial wall is, however, composed only of trophoblast. There is no indication whatever of maternal endothelium lining these innermost foetal lacunae as was suggested by THURSBY-PELHAM. I agree with WISLOCKI and VAN DER WESTHUYSEN that these inner lacunae are lined only by thin strands of syncytial trophoblast.

The method of formation of these lacunae is, moreover, a matter which raised much controversy among earlier workers. PELHAM (1924) regarded them as "arteries", a view which WISLOCKI and VAN DER WESTHUYSEN could not accept. They thought that they must have arisen originally very close to the surface of the endometrium and that "they are probably of the nature of dilated capillaries constituting sinuses which have shed their endothelium" (1940). Actually, indications are that they have been formed in a way which is peculiar only to Procavia. The single layer of cells which constitute the basal trophoblast remains one cell thick in all the uteri studied. Even in the earliest blastocyst stage, however, this basal trophoblast is lined by another layer of much smaller cells on the foetal side. The origin of this layer, which represents the inner trophoblast, has not been observed. Already in this early stage of pregnancy, this layer has started in a few places to form tiny trabeculae which grow outwards, pushing the basal trophoblast slightly away from the inner trophoblast layer and so forming incipient, foetal lacunae. In successively older specimens these trabeculae branch and become more extensive and so the number of foetal lacunae between the inner border of the trophoblast and the basal trophoblast gradually becomes more and more numerous. These lacunae are, therefore, not in the nature of blood lacunae forming between syncytial masses of trophoblastic tissue as they do in Tarsius (HILL 1932), nor do they form "as trophoblastic lacunae by a process of liquefaction of the trophoblast in the manner recently outlined by WISLOCKI and STREETER

(1938) in the macaque", as was suggested by WISLOCKI and VAN DER WESTHUYSEN (1940). Instead, they are definitely constructed and as no cells have been seen originating from the basal trophoblast for this purpose, it seems most likely that the trabeculae are built up by the activity of the cells of the inner trophoblastic layer. The lacunae so formed only become filled with blood in Procavia after the maternal blood-vessels have been penetrated by the trophoblastic papillae. That these inner lacunae are of trophoblastic origin is, however, without doubt true. They are certainly neither "arteries" nor dilated capillaries.

Affinities of Procavia.

Procavia is generally regarded as a primitive Ungulate. Various earlier workers have, however, indicated points of resemblance between this animal and such different groups as the Carnivora, Proboscidea, Sirenia, and Lemuroidea, although no very definite conclusions with regard to its affinities have been attained. It was hoped that the study of earlier stages of embryological and placental development might help to establish some definite relationship. Instead, this present investigation has tended rather to accentuate the rather unique and isolated position which Procavia holds, and to establish yet other links with animals not previously sited as in any way similar to Procavia.

WISLOCKI and VAN DER WESTHUYSEN (1940) have given a comprehensive survey of the opinions of earlier workers. These I shall summarise briefly before discussing the new affinities which early stages have revealed.

MILNE-EDWARDS (1868) and GEORGE (1875) believed that the placenta of the Hyracoidea was of a diffuse, non-deciduate type similar to that of other Ungulata. The present investigation has served rather to substantiate the views of TURNER (1875), ASSHETON (1906), and THURSBY-PELHAM (1924), who instead established its deciduate character.

Several workers found points of resemblance between the placentation of Procavia and the elephant. OWEN (1868) saw a similarity to the decidual, localised and annular form of the elephant's placenta. THURSBY-PELHAM (1924) also speaks of a certain resemblance to the full-term placenta of Elephas. In addition, a review of the fragmentary information supplied by CHAPMAN (1881 and 1899), ASSHETON and STEVENS (1905) and BOECKER (1907) regarding the Proboscidea reveals a relatively close relationship between the placentae of the elephant and the manatee. WISLOCKI (1935) has more recently shown a distinct placental likeness between Procavia and the manatee (Trichechus latirostris) and he, therefore, concluded that "in regard to placentation the Hyracoidea, Sirenia and Proboscidea form a closely related group."

Still other workers have related the placenta of Procavia to that of the Carnivora. OWEN (1868) saw this likeness in the spongy vascular nature of

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the placenta of Procavia, whereas TURNER (1875) said "Hyrax agrees with Felis not only in the form and structure of the placenta but in the presence of a large allantoic sac." WISLOCKI (1930), on the other hand, showed that in certain fundamental ways the placenta of Procavia differs from that of carnivores notwithstanding their common zonary form. The main difference, of course, lay in the fact that in Procavia the placenta is of the haemochorial type, while in carnivores it is endotheliochorial.

Other animals to which Procavia has been related through a study of their placentation are rodents and insectivores (ASSHETON 1906, WISLOCKI 1930), Tarsius (WISLOCKI 1930) and lemurs (WISLOCKI and VAN DER WESTHUYSEN 1940). Tarsius was regarded as having a strikingly similar method of formation of the placental labyrinth, while the lemurs show the same conspicuous and peculiar configuration of the allantois associated with the strange manner in which the allantoic vessels reach the chorion, as in Procavia.

WISLOCKI and VAN DER WESTHUYSEN (1940) have, moreover, pointed out that Procavia has:

1. A central type of implantation with an initial growth of trophoblast over the entire surface of the blastocyst and a subsequent penetration of this trophoblast into the endometrium.
2. A placenta which is at first diffuse but later becomes localised and assumes a zonary shape.
3. A placenta of the haemochorial type.

In respect of the central type of implantation, Procavia, therefore, resembles the Perissodactyla, Artiodactyla, Manidae, Lemuroidea, Cetacea, Carnivora, Bradipodidae, Sirenia and Proboscidea. Of these, however, only the Carnivora, Bradipodidae, Sirenia and Proboscidea have a trophoblast which penetrates the endometrium, and diffuse placentae which later become localised and assume a zonary form. When the finer morphology of the placenta is taken into account, however, the placental affinities of the Hyracoidea become even more restricted, for the Carnivora, and Bradipodidae exhibit endotheliochorial types, whereas the Hyracoidea, Proboscidea and Sirenia are haemochorial.

The present investigation, based on a study of earlier stages has yielded further information. In many respects Procavia bears a striking resemblance to Galeopithecus, with regard particularly to its embryological development. This applies particularly to the formation of a temporary connecting stalk which is, however, not associated with the development of the allantois as it is in some Primates. There is, moreover, a precocious development of mesoderm in both Procavia and Galeopithecus, a feature which they have in common with other animals like Tarsius, Cebus, Elephantulus and man. Amnio-genesis in both Procavia and Galeopithecus is by cavitation as it is in forms such as the hedgehog, Hemicentetes and some Primates.

Procavia has been likened to the lemurs in certain aspects of its placentation.

It does, however, differ in one vital respect at least, viz. that in the lemurs the trophoblast does not become proliferative but simply remains in close apposition to the uterine epithelium, whereas in Procavia the proliferative activity of the trophoblast results in the destruction of the uterine epithelium and the erosion of the endometrial tissues. On the other hand, in the lemurs the chorion is established early and is vascularized precociously and directly by the allantois whereas in Procavia all this occurs very much later, e.g. the allantois only becomes visible in the embryo with 48-somites contained in an uterus which showed a placental swelling of 14.5 mms. diameter.

The actual formation and structure of the ecto-placenta in Procavia is of special interest. Although, when established, the placenta is distinctly haemochorial, its method of formation with special reference to the structure of the trophoblast shows certain features which are not especially characteristic of the typically haemochorial placenta found, for instance, in many Primates. This would account for the fact that a study of fairly late stages of pregnancy seemed to establish a superficial similarity between the method of formation of the placental labyrinth found in Tarsius and in Procavia by WISLOCKI (1930), whereas a study of younger stages has revealed that, in reality, they are not very similar. The trophoblast does, however, in Procavia resemble that of the hedgehog and man in its ability to destroy and resorb the maternal tissues over its whole area instead of in a reduced zone, where the discoidal placentae become established in forms like Macacus, Nasalis and Cebus which have a double discoidal placenta, and in forms like Papio where it is single (HILL 1932).

The general tendency among animals which have a haemochorial type of placenta seems to be that the first attachment to the maternal tissues is achieved by a cellular layer of trophoblast. Subsequently, however, the cellular layer is superseded by a mass of syncytiotrophoblast which invades the endometrium, forms the lacunae and penetrates the maternal blood-vessels, so resulting in the establishment of an ectoplacenta. Thus, in the Pithecoid stage of Primate development, HILL (1932) showed that the ecto-placental trophoblast is at first one-layered but, as soon as it has destroyed the uterine epithelium, it thickens and forms cells towards its outer surface which constitute a syncytial layer and this then invades the endometrium. In rodents like Lepus (DE LANGE 1931), the outer trophoblastic layer of the ecto-placenta also becomes syncytial and fuses with the changing symplasmatic uterine epithelium which it later destroys. In the macaque (STREETER and WISLOCKI 1938) it was also observed that the first attachment of the blastocyst was by means of cellular trophoblast but that after only a few days these cells became indistinct and the conversion to syncytiotrophoblast was commenced, especially in the centre of the implantation area. However, in this animal it is the original cytotrophoblast which

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remains most active for invasion purposes, at the periphery of the implantation area.

A study of the early stages of pregnancy has revealed that in Procavia a very different condition occurs. That part of the trophoblast which forms the initial attachment to the uterine epithelium all round the blastocyst in cellular. Throughout placental development it is this same cytotrophoblast which lies in contact with the maternal tissues, first destroying the uterine epithelium and then gradually penetrating the endometrium where the maternal blood-vessels are also opened. In the earliest stages this trophoblast consists of a single layer of cells called the basal trophoblast which lies in direct contact with the mucosa and an inner zone of cellular, lacunar trophoblast which gradually increases in width as development proceeds. Gradually the parts of this lacunar trophoblast surrounding the innermost foetal lacunae become syncytial, but even in the older stages already described by THURSBY-PELHAM (1924) and WISLOCKI and VAN DER WESTHUYSEN (1940) this syncytiotrophoblast never supersedes the cytotrophoblast as far as the basal trophoblast. Thus, although an ecto-placenta becomes establised in Procavia, which is similar in its ultimate form and functional ability to that which is found in other haemochorial types like Tarsius, the method by which this placenta is established is very different.

Finally, it is worth noticing that in a few respects Procavia seems to show features which do not have their counterpart in any other animals. For instance, the amnion is separated during a considerable period of pregnancy from the chorion by the interposition of a coagulated mass. Implantation is of the circumferential type but is definitely not superficial as is usually the case. The early establishment of an ecto-placenta is not accompanied by the early vascularization of the chorion, nor does the allantois develop early as is the case in most other animals which have a haemochorial type of placenta. Splanchnic mesoderm develops, moreover, before the chorionic mesoderm. Cytotrophoblast and not syncytiotrophoblast is the tissue most active in the formation of the placental labyrinth. The method by which the lacunae are formed in the inner trophoblast is also very different from that which occurs in other animals like Tarsius (HILL 1932), which show the development of an ecto-placenta in the course of placental growth. As mentioned previously, in Procavia the foetal lacunae are formed by the definite growth of trabeculae from the innermost cells of the inner trophoblast. Thus as trabeculae grow and become branched, the basal trophoblast is pushed further and further away from the original layer of inner trophoblast and the foetal lacunar system becomes, as a result, more and more extensive. Only after the blood-vessels are pierced by the trophoblast at the foetal-maternal border are these lacunae filled with maternal blood, thus converting the foetal, lacunar ecto-placenta into a sanguimaternal, lacunar system.

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SUMMARY.

HILL (1932) in his publication on "The developmental history of the Primates" has indicated which characteristics of embryological and placental structure he regards as primitive and which he considers to be highly advanced. It is not for me to say whether these views are completely adequate or correct, but I should like, by way of summarising this investigation on Procavia capensis, to use his standards to demonstrate what a unique position this animal holds. It has, for instance, almost as many highly advanced characteristics as it has primitive ones.

Primitive features of Procavia capensis.

1. Its central method of implantation.
2. There is a marked growth in the size of the blastocyst at an early stage so that it fills the uterine lumen. This results in the formation of a large yolk cavity.
3. The origin and mode of spreading of the mesoderm.
4. The absence of a distinct connecting stalk, except in the very early stages of development.
5. The outgrowth of the allantois in the form of a free, stalked vesicle.
6. The very late vascularization of the chorion.
7. The late development and extension of the extra-embryonic coelom.

Highly advanced features.

1. The direct attachment of the blastocyst to the uterine lining and the very early erosion of the maternal tissue.
2. The persistence of the trophoblast so that the embryonic ectoderm is never exposed at the surface of the blastocyst.
3. Amnio-genesis by the cavitation method, i.e. a "closed" method of amnion formation.
4. Precocious formation of the mesoderm before the primitive streak is visible.
5. The clear differentiation of the trophoblast into cellular and syncytial layers. In Procavia, however, it is the cytotrophoblast which has the erosive and destructive properties and not the syncytiotrophoblast, as is the case in the Platyrrhines and Catarrhines.

Other features of the development and structure of Procavia which may probably be regarded as highly advanced are:

6. The absence of uterine glands in a functional capacity in the implantation area.
7. The haemochorial form of the placenta.

LIST OF ABREVIATIONS.

ac arterial capillary.
acv amnio-embryonic vesicle.
amn amnion.
amnc amniotic cavity.
ar artery.
b body of gland.
ba.tr. basal trophoblast.
bg blastoporal groove.
blc blood capillary.
bl.ex. blood extravasates.
bm basement membrane.
bv blood-vessel.
c crest of trophoblast.
cd cellular debris.
chm chorionic mesoderm.
ci cell inclusions.
coa coagulum.
coam coagulated mass.
cp cytoplasmic process.
cy.tr. cytotrophoblast.
d depression in trophoblast.
dc decidua compacta.
duc degenerating, uterine epithelium.
e endothelium.
ec elongated cell.
ect ectoderm.
embn embryonic node.
emd embryonic disc.
endo endometrium.
ent entoderm.
exc exocoelom.
f fundus of gland.
fl. foetal lacuna.
gl. gland.
gl.epi. glandular epithelium.
gl.l. gland lumen.
Hn Hensen's node.
hpr head process.
in.tr. inner trophoblast.
ips inner periarterial sheath.
lac.tr. lacunar trophoblast (= inner trophoblast).
leu leucocyte.
ls lymph space.
m muscularis.
mbl maternal blood lacuna.
mdc. maternal decidual cell.
mes mesoderm.
mgc multinucleate giant cell.
mit. mitotic.
mm mesometrium.
mor morula.
mym myometrium.
nf neural fold.
ng neural groove.
np neural plate.
oc optic chiasma.
oe oedema.
oe.t. oedematous tissue.
omp omphalopleure.
ov optic vesicle.
p papilla.
pac primary amniotic cavity.
pc predecidual cell.
plac placenta.
pr.st. primitive streak.
rbc red blood corpuscle.
ret reticulum.
s secretion.
sp splanchnopleure.
str. stroma.
sy.tr. syncytiotrophoblast.
tb tail-bud.
tc thickened epithelium.
tp trophoblastic papilla.
tr trophoblast.
ugc uninucleate giant cell.
ut.epi. uterine epithelium.
ut.l uterine lumen.
v vein.
vac vacuole.
vit.v. vitelline vessel.
ys yolk-sac.
zp zona pellucida.

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